

RELATIONSHIP BETWEEN AVAILABLE FISH FOOD, FEEDING HABITS OF FISH AND TOTAL FISH PRODUCTION IN A MICHIGAN LAKE

By ROBERT C. BALL

A dissertation submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in the University of Michigan.

MICHIGAN STATE COLLEGE
AGRICULTURAL EXPERIMENT STATION

SECTION OF ZOOLOGY*

EAST LANSING

**In Cooperation with
Michigan Institute for Fisheries Research*

CONTENTS

	PAGE
INTRODUCTION	3
STUDY OF AVAILABLE FISH FOODS	5
METHODS AND EQUIPMENT	5
Description of Third Sister Lake	5
Physical and Chemical Analysis of Water	7
Sampling of Bottom Deposits	8
Biological Sampling	9
Field Procedure in Sampling of Bottom Fauna	9
Field Procedure in Sampling of Plant Fauna	10
Laboratory Procedure for Plant and Bottom Fauna	11
RESULTS	13
Plant Fauna, 1939	13
Plant Kill, 1940	19
Bottom Fauna, 1939	20
Quantitative Comparisons of Plant and Bottom Samples, 1939	22
Qualitative Comparisons of Plant and Bottom Samples, 1939	23
Bottom Fauna, 1940	24
Bottom Fauna, 1941	26
Seasonal Variation of Invertebrates	29
Comparison of Invertebrate Fauna for 1939, 1940, and 1941	31
Effects of Plant Kill on Invertebrates	32
STUDY OF FEEDING HABITS OF FISH	32
METHODS	32
Procedure for Obtaining Fish	32
Procedure for Analyzing	35
FEEDING HABITS OF FISHES	35
Largemouth Bass	35
Pumpkinseeds	36
Yellow Bullheads	37
Bluegills	37
Forage Ratios	43
SEASONAL RELATIONSHIP OF PLANT FOODS TO INVERTE- BRATE FOODS	45
Relationship Between Coefficient of Condition of Bluegills and Plant Foods Consumed	46
Seasonal Relationship of Invertebrate Foods to Terrestrial Insects	47
Importance of Plankton in Fish Diet	47
Forage Ratios for Plankton	47
DISCUSSION	49
SUMMARY	54
ACKNOWLEDGMENTS	55
LITERATURE CITED	56

A dissertation submitted in partial fulfillment of
the requirements for the Degree of Doctor of
Philosophy, in the University of Michigan.

Relationship Between Available Fish Food, Feeding Habits of Fish and Total Fish Production in a Michigan Lake

By ROBERT C. BALL

In general surveys and investigations of fisheries, the potential fish production of aquatic environments is often evaluated from the volume or number of invertebrates serving as fish food, as determined by sampling methods. To evaluate more adequately the findings of such samplings, it is important to know how the invertebrate population varies seasonally and how it is utilized by the fish of the lake.

In this investigation a study was made of the seasonal variation in the volume and number of invertebrates of a small lake, and these findings were correlated with the feeding habits of certain fishes of the same lake.

Several investigators have considered the relationship of bottom fauna to stream fishes (Surber, 1936, 1938; Davis, 1938; Tarzwell, 1937, but few have related the total bottom fauna to total fish populations, perhaps because of the difficulty of estimating the fish populations in larger bodies of water. The ratio of bottom fauna to the hypothetical weight of fish that could be produced from it has been considered by Richardson (1921). Meehan (1936) and Howell (1941), working with southern ponds of small acreage, determined the weight of fish produced by a known weight of bottom fauna.

The bluegill (*Lepomis macrochirus*) is one of the most abundant fishes in the lakes of Michigan and is one of the most important species to fishermen. This game fish, because of its importance to fishermen and its nearly universal occurrence in lakes of the southern peninsula of Michigan, must therefore be considered in any proposal for fish management. It tends to become very abundant and dwarfed in many lakes, a condition that may be due to a limited food supply. The bluegill does not compete directly for food with most of the other important adult game fishes of the state, but it is widely utilized by many of these game fishes as food. Since the bluegill is important, not

only as a game fish but because of its interrelationships with other fishes in Michigan lakes, a thorough knowledge of the ecological factors contributing to producing a normal growing population of bluegills, such as was present in the lake studied, is necessary.

Preliminary work on this problem was started in the fall of 1938. In April 1939, actual collections of aquatic invertebrates and plankton, of fish for food studies, and of physico-chemical data on the water of the lake, were begun. From that time until the fish were removed by poison in May 1941, sampling, with the exception of fish collections, was carried on at regular intervals throughout the entire year.

Third Sister Lake, Washtenaw County, Michigan, is the largest of a series of three small lakes located near Ann Arbor. It lies in the heart of a forested tract owned by the University of Michigan. It has a surface area of approximately 10 acres, is 60 feet deep, and stratifies chemically and thermally in the summer. There is no permanent inlet, the water entering by a small intermittent stream as runoff from the surrounding hills, which constitute a drainage area of about 320 acres. The outlet flows through a swamp at the west end of the lake and drains into the Huron River, a tributary of Lake Erie. About one-fourth of the shore is sandy gravel and the remainder soft and spongy. With the exception of two limited areas, there is no firm bottom from the shoreline lakeward. The mean slope of the bottom is approximately 20° . The average annual fluctuation of the lake level is between 12 and 18 inches; it reaches its maximum height following the melting of the winter snows and its minimum in late summer. Eggleton (1931) has presented the morphometric data of Third Sister Lake in much greater detail than that given here. Because the lake is a controlled body of water, there has been no extensive fishing in it for many years, and there has been no stocking within the past several years insofar as is known.

For these reasons it was believed that the standing crop of fish represented the maximum for this lake under existing conditions. Age determinations of the game fish of the lake (Brown and Ball 1942a) indicated that the fish were growing at the normal rate for the state of Michigan as tentatively established by Beckman (unpublished); i.e., the bluegills and pumpkinseeds reached legal length in their fourth summer and the largemouth bass in their third summer.

From the beginning of the investigation until its termination, it is

reasonably certain that there were few influences, such as poaching, parasites, or disease epidemics, which appreciably changed the composition of the fish population beyond the limits of its normal fluctuation.

STUDY OF AVAILABLE FISH FOODS

METHODS AND EQUIPMENT

DESCRIPTION OF THIRD SISTER LAKE

In comparing the capacity of lakes such as Third Sister Lake for producing fish, a knowledge of the extent of the area inhabitable by warm-water fishes during the summer months, when their growth is most rapid, is of primary importance. The significant region is that stratum, usually above the thermocline, in which the oxygen content of the water is sufficient to support warm-water fishes and the aquatic plants and animals upon which they depend for food. This is also the region of heaviest plant growth.

Third Sister Lake may be divided, more or less arbitrarily, into four zones, as illustrated in Figs. 1 and 2.

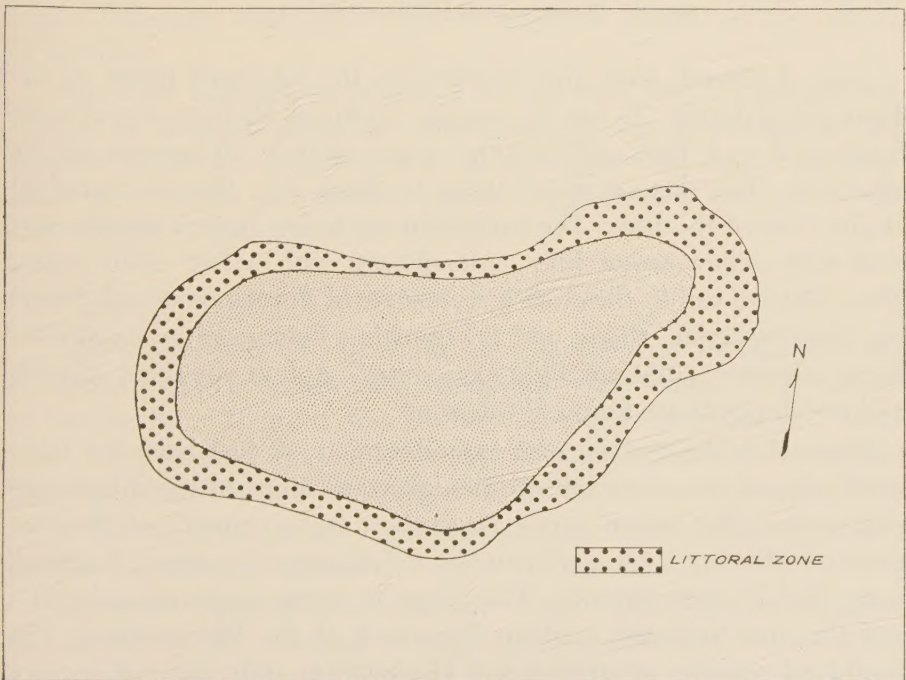


Fig. 1. Surface view of Third Sister Lake.

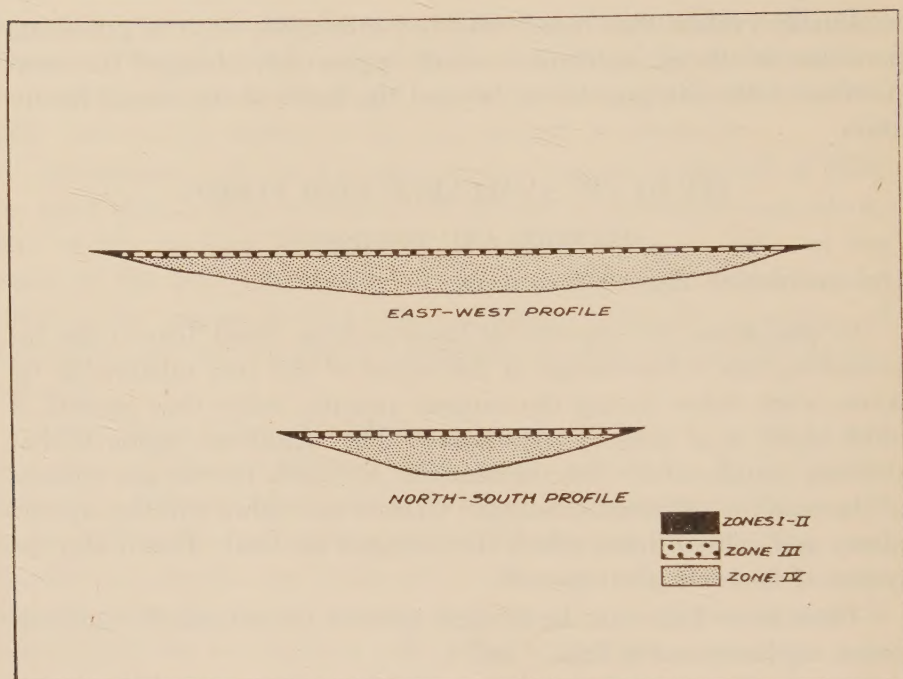


Fig. 2. Profile views of Third Sister Lake.

Zone I extends from the shoreline to the lakeward limits of the floating vegetation. It has an average width of 30 feet, a maximum depth of 5 to 6 feet, and includes approximately 30 percent of the lake area. The slope of the bottom is about 13° , the most gradual of any zone of the lake. The surface of the water here is largely covered with yellow water lilies, interspersed with a few white water lilies. Bottom soil in this area is a mixture of fibrous peat and decaying plant material. *Chara* and low-growing *Potamogeton amplifolius* occur wherever sufficient light penetrates. A few emergent aquatic and marsh plants are found in this zone.

Zone II is the narrow zone extending 8 to 12 feet from the lakeward edge of the water lilies to the lakeward limits of the submerged vegetation. This entire region supports a heavy growth of *Potamogeton amplifolius*, with spare patches of *Potamogeton natans*, *P. gramineus*, and *P. zosteriformis*. The slope is steep, approximately 31° , and the area included is about 5 percent of the lake surface. The combined volumes of zones I and II constitute only about 6 percent of the total lake.

Zone III is the stratum enclosed horizontally by the lakeward limits of the vegetation zone and vertically by the upper limits of the thermocline. This stratum is of importance in producing fish-food only because of the plankton found there. Fish can inhabit this region but were not commonly present there, apparently preferring to stay nearer the protection and food sources of the plant zones. This zone includes approximately 65 percent of the lake surface and 26 percent of the lake volume.

Zone IV is the basin of the lake below the 10-foot contour. On the basis of data obtained in the study of food used by fish, this region was considered of minor importance in the production of fish food. The potential food organisms occurring here are *Chironomus utahensis* and perhaps other closely related forms, *Chaoborus* (*Corethra*), and the aquatic oligochaetes. These midges and annelids were present in large numbers below the thermocline in the oxygen-impooverished waters where the fish do not feed; they therefore were not available as food except during the emergence period of the insects. As will be shown later, the *Chaoborus*, although probably available during part of their diurnal cycle, were not utilized extensively as food. This zone constitutes approximately 68 percent of the volume of the lake.

From the descriptions above it can be seen that the region considered as of most immediate importance in the production of fish food for this lake is the plant zone, 35 to 40 feet wide, around the periphery of the lake. It comprises about 35 percent of the area of the lake and only 6 percent of its volume.

PHYSICAL AND CHEMICAL ANALYSIS OF WATER

The temperature of the water was measured at 2-week intervals throughout the investigations. Readings were taken from surface to bottom by a Negretti and Zambra reversing thermometer. Third Sister Lake stratifies thermally during the summer, with a thermocline between 12 and 21 feet, varying in its limits depending on the date.

Water samples for all chemical analyses were collected with a modified Kemmerer sampler.

Dissolved oxygen was determined by the Rideal-Stewart modification of the Winkler method as outlined in *Standard Methods for the Examination of Water and Sewage* (1936). The oxygen concentration in the littoral zone remained, throughout the year, well above

the minimum demanded by warm-water fishes. During the late summer, the oxygen became depleted in the waters below the thermocline.

Free carbon dioxide was determined with N/44 KOH and phenolphthalein as outlined in *Standard Methods for the Examination of Water and Sewage* (1936). Free carbon dioxide was seldom present in the upper 10 feet of the water during the summer, and rarely exceeded 15 p.p.m. in the deepest water.

Carbonate and bicarbonate determinations were made according to the outline in *Standard Methods for the Examination of Water and Sewage* (1936). Phenolphthalein alkalinity was seldom present, and the methyl-orange alkalinity varied but little, ranging between 85 and 95 p.p.m., from surface to bottom, during most of the summer.

The hydrogen-ion concentration was determined by a Hellige colorimeter. The pH range for the summer was from 7.2 to 8.4 for surface waters, but the pH dropped to 6.8 at the greatest depths during late summer.

SAMPLING OF BOTTOM DEPOSITS

The character of bottom deposits in the littoral zone was determined from samples taken, in most areas, with an Ekman dredge. A Peterson dredge was operated in restricted gravel areas where the Ekman dredge would not function properly. The Ekman dredge, by taking a smaller and less bulky sample, made possible the collecting and sorting of larger numbers of samples than would have been possible with the Peterson dredge, thus giving a better representation of the bottom fauna. The Peterson dredge has a collection area of 0.826 square foot, and the Ekman samples 0.25 square foot. All samples were taken from a boat; a rowboat crane (Brown and Ball, 1940) was used to facilitate handling of the dredges.

To establish the exact location of collecting stations, the shoreline was divided by posts into approximately equal sections, the markers being about 40 yards apart. Samples were taken within the 10-foot contour along transects extending from these posts to the center of the lake. Preliminary bottom sampling and analyses of contents of fish stomachs indicated that the area within the 10-foot contour was furnishing the bulk of the fish food. This depth also coincided with the upper limit of the thermocline during much of the summer, and netting operations showed the movement of the fish

to be largely, if not entirely, limited to the region of the lake above the 10-foot level.

Dredge samples showed that the bottom material of the littoral zone was predominantly fibrous peat containing large amounts of organic material. The sublittoral zone was composed of a clean fibrous plant material containing some organic matter. Below this the lake floor was blue clay overlaid with a thin layer of organic ooze.

BIOLOGICAL SAMPLING

During the period from April 1939 to May 1941, bottom samples were taken during every month of the year. A few regular collection dates were changed during the period of freezing-over in the fall and during the break-up period in the spring when the ice was unsafe. This study is concerned, however, only with those samples collected during the ice-free period of the year. During the periods from April 15 to November 1 of 1939 and 1940, and April 1 to May 1, 1941, 458 dredge samples were collected in the littoral zone. In addition to the dredge samples, 103 pounds of submerged aquatic plants were collected from the zone under consideration for qualitative and quantitative studies of the invertebrate population. Besides these, many samples were collected in the region below the 10-foot contour. These deep-water samples are not tabulated here, as their purpose was to familiarize the writer with the organisms present below the main area sampled so that they might be recognized if found in the fish stomachs. The deep-water samples showed the important organisms, as far as bulk was concerned, to be *Chaoborus*, *Chironomus*, and *Oligochaeta*. Of these three groups only *Chironomus* were utilized as food to any extent, and they constituted a very small percentage of the midges taken as food. *Chironomus utahensis* taken as food were, almost without exception, mature pupae, indicating that they were rising to emerge when captured.

FIELD PROCEDURE IN SAMPLING OF BOTTOM FAUNA

As has been mentioned, bottom samples were obtained by lowering an open dredge to the lake bottom from an anchored boat. After the dredge was closed, it was raised until its top was at the surface of the water. Then a fine-mesh screen pan was placed beneath the dredge (under water), and both were lifted into the boat. Contents of the dredge, along with any material caught in the screen, were

transferred to a pail and taken to shore for washing. All material that would go through a 30-mesh sieve was washed out. The residue containing the organisms and trash was poured into a glass fruit jar, taken to the laboratory, and picked over while the organisms were alive. Whenever possible, invertebrates were taken from the samples, measured volumetrically, and in many cases weighed, alive. When time did not allow weights and measurements to be made on living material, it was preserved in 80-percent alcohol for identification and measurement at some later date.

FIELD PROCEDURE IN SAMPLING OF PLANT FAUNA

It was believed that any survey of fish foods would not be complete unless those organisms inhabiting the higher aquatic plants were considered. As no practical method of quantitatively collecting plants, applicable to fisheries field investigation, was known to the writer, an attempt was made to determine quantitatively and qualitatively the invertebrate fauna of the plant beds from plant samples collected by a plant hook.

To collect a plant sample, the boat was anchored over a submerged plant bed. A plant hook was thrown into the bed, drawn slowly towards the boat until approximately 3 pounds of plants had been secured, and then brought to the surface. The plants were not lifted from the water until a fine-mesh screen pan had been placed under them, since it was found that the largest determinable loss of organisms occurred when lifting the plants from the water. They were then placed in a tub, along with any material in the screen, and taken to shore for washing and weighing. There the plants were piled loosely in a 30-mesh sieve, drained for 5 minutes, and weighed. This was the "wet weight" and included plants, encrusted marl on plant stems and leaves, and sometimes small amounts of bottom material adhering to the plants. Next, the plants were transferred to a tub of clean water and the marl, other debris, and most of the plant-dwelling invertebrates washed off. They were then washed through five separate pails of clean water and again piled loosely on a fine-mesh screen for draining and inspection for complete removal of organisms. Plants were allowed to remain spread out 5 minutes before being weighed.

Water containing the invertebrates from the plants was then poured through a 30-mesh screen and the debris drained 5 minutes. The resi-

due, consisting of broken plant parts and fish-food organisms, was weighed and this weight included with that of the washed plants. This was considered as the "washed weight" and represented the plants and organisms on them but not extraneous material, the weight of which varies according to the season, water conditions, and collecting methods. This weight was used in all calculations as it is believed that it has a more constant relationship to the invertebrate fauna than wet weights, in that collection methods and other factors do not influence it as much. Washed plant material was then discarded and organisms and accompanying trash taken to the laboratory and sorted while the organisms were still alive. These plant-inhabiting invertebrates were then treated as outlined for bottom fauna collected by dredge.

This method of estimating the standing crop of invertebrate fauna of plants is open to many criticisms, but, as outlined, is one applicable to field use with a minimum of equipment. If sufficient samples are collected and the same procedure for collecting each sample is carefully followed, errors are reduced, and the method can serve as a useful addition to dredge sampling in estimating the fish food in a lake.

LABORATORY PROCEDURE FOR PLANT AND BOTTOM FAUNA

Workers in this field have used several different methods for making quantitative measurements of organisms from bottom samples but to date no one method seems to have been accepted by the majority. In quantitative determinations of bottom fauna, the weight method has little advantage over the volumetric method, unless the worker incinerates each sample to get the organic weight only. That weight, at present, is rather meaningless in the absence of physiological data on the nutritive value of the organic elements of the various organisms. Accurate weighing is impracticable in the field and is time-consuming in the laboratory. Practical considerations greatly favor the volumetric method. It is the only method suitable for field use; it does not require special, costly, or delicate apparatus, and it is rapid compared with weighing. Data obtained in this study indicate that one can convert cubic centimeters of volume to grams of weight with but small error so far as invertebrate organisms are concerned, for after all, the errors inherent in the best methods of bottom sampling are large, almost certainly large enough to obscure any error introduced by the conversion.

The organisms to be measured were placed in a graduated centrifuge tube which had previously been calibrated against a burette having the same graduation values. The tube was then placed in a rack which held it with the mouth of the tube down, at a 45° angle, and allowed to remain there 3 minutes. This allowed the liquid to drain off, but the specimens did not lose moisture by evaporation, an important matter when working with material preserved in alcohol. It was found that this method permitted eliminating much of the variation inherent in all methods used to reduce moisture to a near constant, prior to making volumetric or wet-weight determinations of bottom fauna. When active organisms were being measured, a wire-gauze plug was inserted in the tube to keep them from crawling out. This plug did not interfere with the draining of moisture and was removed just prior to the next step. The tube and its contents were then placed under the burette, and enough liquid to cover the sample was allowed to run out. The difference between the reading on the burette and the reading on the centrifuge tube was the volume of the invertebrates. This method was checked against other methods of volumetric analysis and found to be more rapid and accurate for this work.

The volume of the entire bottom sample was determined; then the sample was divided into taxonomic groups, and each group was measured separately in the same manner as the whole sample.

Following the volumetric measurements, numerical counts of all organisms were made, and the invertebrates were identified as far as was believed necessary for this study.

It was found that volumetric measurements of single specimens of the smaller invertebrates encountered in bottom and plant samples were not accurate within the limits desired. To minimize this error, large numbers of these organisms, within a given size range, were measured, and an average volume for each individual was calculated. This calculated volume was used whenever small individuals or groups of individuals having a small volume, were to be measured. All measurements were made on invertebrates preserved more than 2 months in 80-percent alcohol. The lengths were determined by straightening the organism and measuring the greatest overall body length. Case length only was taken for all Trichoptera. Snails were measured along the greatest diameter of the shell. For the larger dragonflies, the variation in width made any estimate based on a single measurement unreliable, and for that reason both the width and length were taken. Measurements of the larger organisms were

made for completeness of the table but were not used in actual computation of volume.

To compare the data obtained in this study with those of certain other investigators, it was necessary to convert the volume of invertebrate organisms to grams of wet weight. As it was not possible to determine live weight on most bottom samples, a conversion factor was worked out for changing volume in cubic centimeters, as determined from organisms preserved in alcohol, to an equivalent live weight in grams.

Several series of quantitative samples were collected, the organisms weighed, and their volume determined while they were still alive. This material was preserved in 80-percent alcohol, sealed, and set aside for approximately 6 months. It was then considered as having received preservation treatment comparable with that of the invertebrate samples collected throughout the investigation. Volumetric measurements were then made.

As nearly as possible, representative invertebrate samples were selected for these experiments. From these data it was found that there is more variation between live weight and live volume than between live weight and preserved volume. For all groups of organisms considered, the conversion factor for changing preserved volume in cubic centimeters to an equivalent live weight in grams is 0.98. Therefore, for purposes of this study, 1 cc. of preserved volume can be considered the same as 1 gram live weight.

RESULTS

PLANT FAUNA, 1939

The aquatic plants found in Third Sister Lake are listed in Table 1. Of these 28 species, *Potamogeton amplifolius* constituted approximately 90 percent of the submerged vegetation of the lake. This estimate was based on the density of the plant beds and the area they covered.

Collection of plants was carried out during the summer of 1939 and resumed as soon as they appeared in the spring of 1940, which was in the latter half of May. In June of that year a phenomenon, which will be referred to in this paper as "plant kill" and which will be described later, interfered with the normal growth of the plants. Because of the action of this plant kill, plant sampling could not be carried on in the summer of 1940, consequently, data on plant inhabiting fauna were accumulated only for the year 1939.

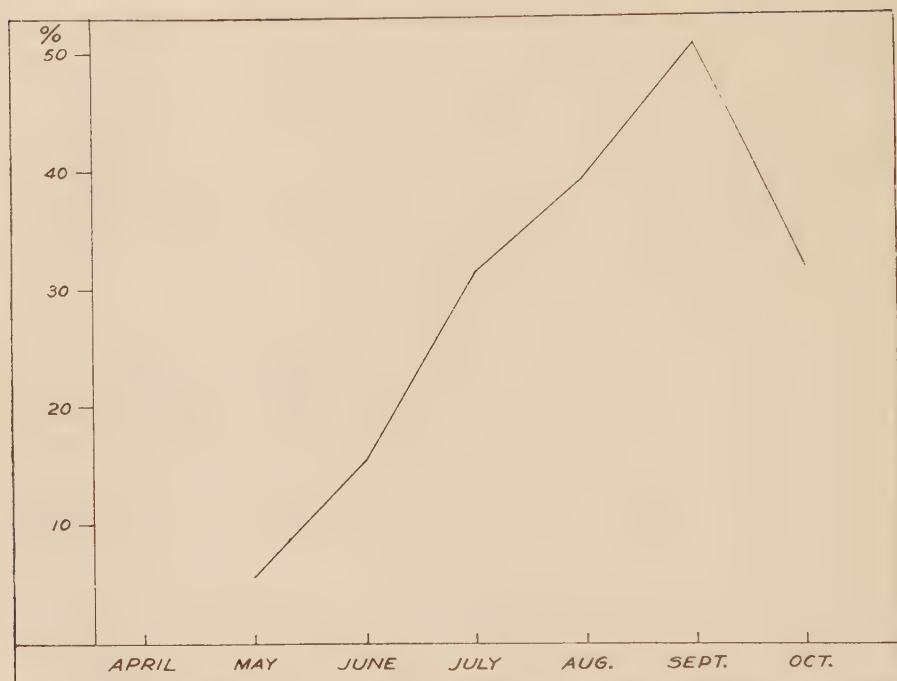


Fig. 3. Percentage of marl in total weight of *Potamogeton amplifolius* in Third Sister Lake.

Plants collected to furnish data on the invertebrate fauna of the lake were treated as previously described, i.e., the plants were drained and weighed, marl and accumulated debris were washed off, and the plants were again weighed. It was found that marl deposition on the plants increased steadily as the summer progressed. The percentage of marl accretion is shown in Fig. 3. Collections of plants were started when the plants were first large enough to be taken with a

TABLE 1—Aquatic plants in Third Sister Lake*

Asclepias incarnata
Alisma Plantago-aquatica
Carex sp.
Ceratophyllum demersum
Chara sp.
Dulichium arundinaceum
Eleocharis Smallii
Eleocharis pauciflora
Eupatorium perfoliatum
Equisetum fluviatile
Heteranthera dubia
Leersia oryzoides
Lysimachia thyrsiflora

Mimulus ringens
Najas flexilis
Najas gracillima
Nuphar advena
Nymphaea odorata
Potamogeton amplifolius
Potamogeton gramineus
Potamogeton natans
Potamogeton zosteriformis
Penthorum sedoides
Ranunculus pennsylvanicus
Scirpus acutus
Typha latifolia

*Plants collected and identified by Betty Robertson Clarke.

plant hook. At this time the marl encrustation on the plants was very light and constituted about 5 percent of the weight of the plants. Weight of the marl increased at a uniform rate throughout the summer, until early in September marl on the plants weighed as much as the plants themselves. At this time the water began to cool, the plants gradually declined, and the marl broke off. It does not seem that the marl deposition on the plants in this lake, whose water was moderately hard (M.O. alkalinity 85-95 p.p.m.), has any marked effect on plant growth, as the beds of *P. amplifolius* were very dense. The marl may have a hastening effect on the decline of plants. When they began to show signs of deterioration, the decline was very rapid for most of them, the exception being those plants that were subjected to some wave action which broke off the marl. These plants remained until after the ice cover was formed, staying green for several weeks under clear ice.

In this paper, the invertebrate fauna determined by plant sampling are treated separately from the invertebrate fauna determined by dredge sampling. Species names of invertebrates have not been used in the body of this paper. They have no explicit purpose in this problem, and specific determinations cannot be made, in most instances, when handling large numbers of organisms daily, even if the worker were qualified to make them. In most cases identifications were carried as far as deemed necessary and practicable for this study, usually only to family groups. Nearly all of these could be identified in the field.

Data from the plant sampling done in 1939 are presented in Table 2. Pertinent data from the collections, including the number and volume of organisms per pound of washed plants, have been summarized in the top half of the table. The measured number and volume of organisms, as well as the percentage of total number and volume for each organism for each collection period, have been tabulated in the lower portion.

Dragonfly nymphs of three taxonomic groups, the aeschnines, libellulines, and gomphines, were tabulated separately in both plant and bottom sampling collections as an aid in determining whether qualitative differences in the fish-food crop are shown equally by the two methods of sampling. Trichoptera collected were predominantly *Leptocella albida*, one of the Leptoceridae that builds a cone-shaped portable case of silk, shingled with small stones. How much of this

TABLE 2—*Invertebrate fauna collected by plant sampling in 1939*

Collection dates.....	May	June	July	August	September	October	
Number of samples...	3	3	5	9	7	4	31 (total)
Drained weight (lb.)...	4.5	6.9	12.9	39.9	31.7	14.0	110 (total)
Washed weight (lb.)...	4.25	5.8	8.95	24.0	15.7	9.6	68.3 (total)
Percent loss.....	5.5	15.4	30.9	39.8	50.5	31.2	
Total number of organisms.....	743	210	534	1762	650	413	4312 (total)
Number of organisms per lb.(washed weight)	175	36.1	53.4	73.5	41.2	43.0	53.1 (average)
Total volume of organisms (cc.).....	8.23	2.87	4.55	34.66	21.76	13.64	85.71 (total)
Volume of organisms per lb.(washed weight)	1.92	.50	.51	1.44	1.38	1.42	1.25 (average)
Libellulidae.....A	9 1.22	5 2.38	5 .97	70 3.97	34 5.23	25 6.05	3.43
B	.45 5.49	.45 15.67	.17 3.73	5.74 16.56	4.36 20.03	2.64 19.35	16.09
Gomphinae.....A	2 .27	1 .47	3 .56	37 2.10	31 4.77	3 .73	1.79
B	.18 2.20	.05 1.74	.39 8.57	3.13 9.03	3.33 15.30	.63 4.62	8.98
Aeschninae.....A				6 .34			.14
B				.87 2.51			1.01
Zygoptera.....A	94 12.69	5 2.38	4 .75	198 11.23	164 25.23	53 12.83	12.08
B				1.09 3.14	2.09 9.60	.56 4.10	5.90
Trichoptera.....A	123 16.61	66 31.42	191 35.76	967 54.88	285 43.84	160 38.70	41.57
B	4.00 48.80	1.70 59.23	1.82 40.00	19.86 57.29	8.96 41.17	7.95 58.27	51.64
Midges.....A	358 48.33	46 21.90	241 45.13	247 14.01	47 7.23	140 33.88	25.03
B	1.15 14.03	.17 5.92	.90 19.78	.66 1.90	.20 .91	.53 3.88	4.21
Snails.....A	122 16.47	75 35.71	27 5.05	142 8.05	74 11.38	27 6.53	10.83
B	1.07 13.05	.35 12.19	.27 5.83	1.91 5.51	2.15 9.88	.67 4.91	7.48
Leeches.....A	4 .54	4 1.90	.15 2.80	31 1.75	6 .92	3 .73	1.46
B	.06 .73	.12 4.18	.39 8.57	.87 2.51	.45 2.06	.66 4.84	2.97
Ephemeroidea.....A	3 .40		18 3.37	7 .40	1 .15	1 .24	.70
B			.15 3.29				.18
Hyalaele.....A	18 2.43	3 1.42	6 1.12	27 1.53		1 .24	1.28
B	.04 .49			.03 .08			.08
Other Diptera.....A			14 2.62	20 1.13			.79
B			.16 3.51	.03 .08			.22
Tabanidae.....A		1 .48	3 .56	3 .17			.16
B			.25 5.49	.40 1.15			.76
Pisidium.....A				3 .17	2 .31		.12
B				.04 .11	.02 .09		.07
Lepidoptera.....A	10 1.35	3 1.42	3 .56	1 .06	2 .31		.53
B							.40

A=Number of organisms and percent of all organisms by number.

B=Volume of organisms in cubic centimeters and percent of all organisms by volume.

case, exclusive of the stones, is of value as food is not known, although the case is digestible. For this reason, as well as for the time required to remove the caddis worm from the case, measurements of the Trichoptera include the case. A factor for the conversion of total volume of case and caddis to the volume of larvae alone was determined as

0.45. This factor was applicable to all sizes of this species of insect but was not used in this study.

No effort was made to separate midges from plant samples into taxonomic groups as the time necessary for identification of these, if such identification were possible, could in no way be justified for this investigation.

In tabulating the volume of invertebrates per pound of plants, it was seen that the peak, for the period under consideration, occurred in early spring. Following this there was a rapid decline in the total volume, until a minimum was reached during the latter part of June and the first part of July. The period of decline coincides with the emergence period of many of the aquatic insects. The period of recovery, although rapid, is somewhat slower and by October 15 does not reach a volume as great as that of the early part of the season. These data, presented graphically, are shown in Fig. 4. On this same chart is also shown the variation throughout the summer in numbers of organisms per pound (washed weight) of *P. amplifolius*. From

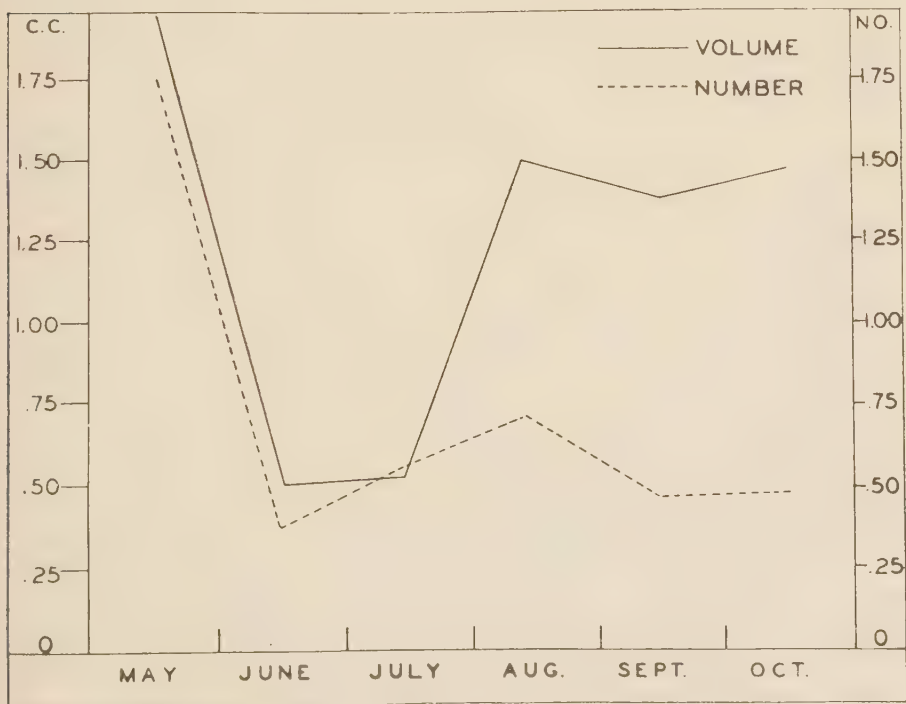


Fig. 4. Seasonal variation of invertebrate organisms on *Potamogeton amplifolius*, 1939.

this chart it is seen that there was a high point in early spring, followed by a rapid drop to a minimum in June. From this period on there was an increase in numbers until the middle of September, when another decrease took place. The number of organisms per pound of plants was dominated to a considerable extent by the midge population, which in Third Sister Lake has its chief emergence period in May and one of lesser magnitude in mid-September.

The volume curve (Fig. 4) shows the effect of the second emergence but slightly, possibly because bulky organisms such as the dragonfly nymphs and caddis larvae that do not emerge until the following year are increasing rapidly in body volume throughout this period.

The most abundant organism, both by number and by volume, was the caddis. This insect outnumbered even the ever-present midge larvae on the plants of the lake, and comprised nearly twice the volume of the nearest other group, the libelluline dragonflies. The caddis larvae constituted 51 percent of the total volume and 42 percent of the total number of all organisms. Next in importance in number and volume were the dragonflies, followed by damselflies, snails, midges, and leeches in the order named. None of the other invertebrates made up more than 1 percent of the total. The percentage composition, by number and volume, of the plant-inhabiting invertebrates is shown in Fig. 5.

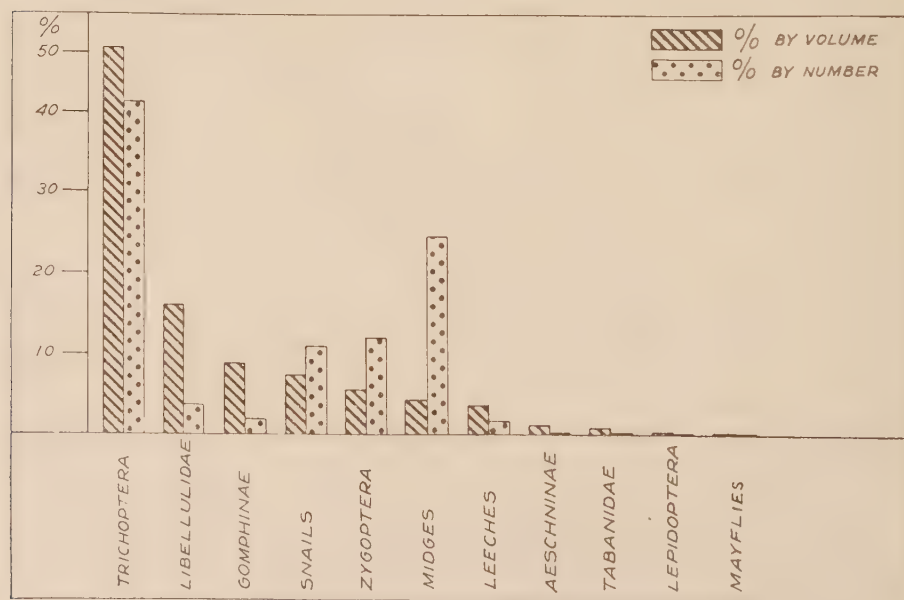


Fig. 5. Percentage composition of plant fauna, volume and number, 1939.

Klugh (1926) has summarized the literature dealing with the significance of aquatic plants and has proposed that rooted submerged vegetation has possibilities as an index of a lake's potential productivity. Surber (1930), in a study of the number of organisms per square meter on areas of slough bottoms which supported larger aquatic plants, found that the number of organisms present in vegetated zones was far greater than in zones where no vegetation grew. Needham (1928) collected square-foot samples of submerged plant beds to ascertain the relative value of such beds in trout streams and concluded from his studies of the fish-food organisms taken from these samples that plant beds were approximately 7 to 35 times as rich in fish food as comparable areas without plants. Pate (1933), in an investigation similar to that of Needham, came to the same conclusions.

PLANT KILL, 1940

In 1940, as was mentioned above, plant collections were begun in the latter half of May. For the first 3 weeks of June, the *Potamogeton amplifolius* made rapid growth and assumed nearly maximum size for this lake.

During the last week of June the water became quite warm (78° F.), and large masses of filamentous algae were seen floating in the lake. Soon afterwards, an unusual growth was seen on and about the leaves of the plants. It increased rapidly and by the first week of July had enveloped the plants with a transparent gray-green veil. As far as could be determined, every plant of *P. amplifolius* in the lake was so affected. This covering was not found on other plants. Small beds of *Potamogeton natans* and *P. zosteriformis* were not affected in any manner. The growth continued until the entire submerged plant zone, with the exception of small patches of other species, appeared veiled with it.

Stems and leaves of the plants maintained their position in relation to the original plant and to the lake bottom, probably due to buoyancy of the algal mass incorporated in, or constituting, the plant covering. A plant hook thrown into and dragged through what appeared to be a heavy bed of plants would come up bare, or at most with a few strands of rotted plant material. The plants turned a dead brown color with no green showing. This condition was reached by July 20. From that time until late August the plants gradually fell apart, the lower leaves going first. Finally only stems remained, and many of these were decomposed. Decomposition of the stem proceeded from top to bottom.

After the leaves were completely lost, there was a dormant period, during which there was no sign of life in this plant in the entire lake.

After about 10 days, small leaves began to appear on the tips of the stems remaining erect. There were no signs of any new stems coming from seeds or roots. Growth of these new leaves was rapid and continued until individual plants assumed a nearly normal appearance for this lake, except that they were much shorter, possibly because nearly all stems had suffered some decomposition at the tip before regeneration began. The plants appeared to grow until about the middle of November. At this time the original plant beds were outlined, but less than one-third of the normal plant population was present in the lake.

The material surrounding the plants was preserved as soon as it was known that the plants were being affected. This was examined, and several species of algae were identified, most common among them being *Rhizoclonium* and *Bulbochaete*. None of the algae found are known to be parasitic on, or to attack, higher plants, and inquiry at the time failed to disclose any knowledge of such a condition occurring naturally on a large scale. A very similar condition, however, has been described by Swingle and Smith (1942) as a phase in the intentional destruction of aquatic plants in fish ponds. The condition described by them was the result of fertilization of the ponds that caused an increase in filamentous algae, which covers the plants and shades them to the extent that they weaken and die. If the algal increase on the plants in Third Sister Lake was due to an increase in nutritive material, its source was not determined.

General observations indicated that aquatic insects normally inhabiting *P. amplifolius* were living on the lake bottom in areas formerly occupied by plant beds. The insects did not return to the plants until the plants were again almost fully leaved. These plants offer little protection until almost full-grown.

This phenomenon, which nearly wiped out the submerged aquatic vegetation of Third Sister Lake for part of a summer, prevented gathering data for comparison with the 1939 plant collections, and also stopped experiments on methods of taking quantitative samples of aquatic plants.

BOTTOM FAUNA, 1939

During the summer of 1939, dredge samples were taken in the littoral zone in the same general region and at approximately the

same times as the plant samples. These samples were processed as indicated previously, and the invertebrate fauna from them were tabulated by number and by volume per square foot. It was impossible in Third Sister Lake to collect dredge samples in most parts of the littoral zone without including some plant material, and consequently the dredge collections represent not only the bottom-dwell-

TABLE 3—*Invertebrate fauna collected by dredge sampling in 1939*

Collection dates.....	May	June	July	August	September	October	
Number of samples...	2	2	5	8	2	15	34 (total)
Total area in samples (sq. ft.).....	1.65	1.65	4.13	5.45	1.65	6.05	20.58 (total)
Total number of organisms.....	73	25	220	368	27	422	1135 (total)
Number of organisms per sq. ft.....	43	15	53	66	16	70	55 (average)
Total volume of organisms (cc.).....	1.03	1.43	3.25	6.91	2.29	10.59	25.50 (total)
Volume of organisms per sq. ft.....	.63	.87	.79	1.27	1.39	1.75	1.24 (average)
Libellulidae.....A			15 6.83	38 10.24	3 11.10	22 5.21	6.87
B			.91 28.02	2.00 29.00	.37 16.17	2.32 21.90	21.95
Gomphinae.....A	6 8.22	5 20.00	5 2.28	13 3.54	3 11.10	17 4.02	4.32
B	.43 41.70	1.10 76.89	.75 23.10	1.25 18.13	.56 24.47	1.36 12.84	21.36
Aeschninae.....A			2 .91			1 .23	.26
B			.05 1.54			.35 3.30	1.57
Zygoptera.....A	1 1.37		2 .91	87 23.66		43 10.18	11.72
B				.26 3.77		.44 4.15	2.72
Trichoptera.....A	10 13.70		41 18.66	126 24.72	7 25.90	91 21.56	24.23
B	.30 29.13		.47 14.48	2.36 34.22	.24 10.49	3.57 33.71	27.20
Chironomidae.....A	40 54.80	12 48.00	117 53.24	49 13.33		27 6.39	21.58
B	.10 9.71	.01 .70	.43 13.24	.15 2.17		.29 2.74	3.84
Snails.....A	6 8.22	5 20.00	9 4.10	20 5.44		24 5.68	5.64
B	.05 4.85	.02 1.40	.05 1.54	.10 1.45		.40 3.77	2.43
Leeches.....A	1 1.37	3 12.00	5 2.27	1 .27	4 14.80	6 1.42	1.76
B	.08 7.77	.30 20.97	.27 8.32		.50 21.85	.80 7.55	7.64
Ephemerae.....A	4 5.48		8 3.64	4 1.09		81 19.19	8.55
B	.01 .97		.01 .31			.43 4.06	1.76
Hyalella.....A	2 2.74		10 4.55	24 6.53		91 21.56	11.19
B			.01 .31	.01 .15		.13 1.23	.50
Gammarus.....A						14 3.31	1.23
B						.32 3.02	1.25
Tabanidae.....A			3 1.37	6 1.63		2 .47	.97
B			.29 8.93	.78 11.31		.15 1.41	4.78
Coleoptera.....A					10 37.00		.88
B					.62 27.09		2.43
Pisidium.....A						3 .71	.26
B						.03 .03	.11
Oligochaeta.....A	3 4.11		3 1.37				.53
B	.06 5.83		.01 .31				.27

A = Number of organisms and percent of all organisms by number.

B = Volume of organisms in cubic centimeters and percent of all organisms by volume.

ing organisms but also a small unknown percentage of invertebrates from plants. All organisms taken by a dredge in this investigation will be referred to as bottom fauna.

From the bottom-sampling data in Table 3 it can be seen that, volumetrically, the principal constituents of the bottom fauna were the dragonfly nymphs, Trichoptera larvae, leeches, and midge larvae, named in order of decreasing volume. The first two groups constitute nearly 70 percent of the bulk of the macroscopic bottom fauna. Others listed in the table were either small organisms that require large numbers of individuals to form an appreciable volume, such as the mayflies and Hyalella, or larger ones, such as *tabanid* and Coleoptera larvae, that appear infrequently in the samples. The organisms of this latter classification may be volumetrically significant in a few collections but not when considering the average of the standing crop of fish food for the entire summer.

QUANTITATIVE COMPARISONS OF PLANT AND BOTTOM SAMPLES, 1939

Data from the 1939 plant and dredge samples have been tabulated in Table 4 and a comparison made of the volume of invertebrates per pound of plants with the volume of organisms per square foot of lake bottom. From this table it can be seen that 1 pound of plant material ("washed weight") is approximately equivalent to 1 square foot of lake bottom as a producer or harbinger of fish-food organisms. This conclusion is based on the averages of all collections taken throughout the summer. The number of dredge samples on which these data were based was small. However, comparative values

TABLE 4—Comparison of volume of organisms per pound of plant material with volume of organisms per square foot of lake bottom, 1939

	Dredge samples	Plant samples
Number of samples.....	34	31
Size of samples.....	20.58 sq. ft.	110 pounds* 68.4 pounds**
Total number of organisms.....	1135	4313
Number of organisms per unit.....	55 per sq. ft.	44 per pound* 63 per pound**
Total volume of organisms.....	25.6 cc.	85.8 cc.
Volume of organisms per unit.....	1.2 cc.	0.8 cc.* 1.3 cc.*

*Based on drained weight.

**Based on washed weight.

based on dredge samples and plant samples from heavy beds of *P. amplifolius* may be of value in estimating the available food in lakes where dredge sampling cannot be carried out because of heavy vegetation interfering with the action of the dredge, extreme declination of the lake bottom, or other factors.

QUALITATIVE COMPARISONS OF PLANT AND BOTTOM SAMPLES, 1939

It is generally considered that lakes having extensive zones of submerged vegetation are more productive of warm-water fishes than lakes poor in vegetation.

The quantitative sampling of invertebrates inhabiting zones of submerged vegetation has been neglected in the past in favor of dredge sampling as a means of determining the possible fish-food supply of lakes. The methods of dredge sampling are better established, and the findings of many workers who have used such methods are available for comparison.

One of the aims of this investigation was to determine whether bottom sampling alone was adequate to estimate the invertebrate fish-food supply of a lake or whether certain elements were being overlooked.

A qualitative comparison of results obtained by the two methods of sampling is presented in Table 5. A comparison of the percentage composition by number shows that the dragonflies taken by dredge sampling were approximately twice as abundant in relation to other forms as they were in plant samples. Leeches, damselflies, and midges were present in about equal proportions in both types of samples; caddis and snails were proportionately about half as abundant in

TABLE 5—Comparisons of invertebrate fauna collected in dredge and plant sampling, 1939

	Percent by number		Percent by volume	
	Plant samples	Dredge samples	Plant samples	Dredge samples
Libellulidae.....	3.0	7.0	16.0	22.0
Gomphinae.....	2.0	4.0	9.0	21.0
Aeschninae.....	.1	.3	1.0	1.5
Zygoptera.....	12.0	12.0	6.0	3.0
Trichoptera.....	42.0	24.0	52.0	27.0
Midges.....	25.0	22.0	4.0	4.0
Snails.....	11.0	6.0	8.0	2.0
Leeches.....	1.0	2.0	3.0	8.0
Hyphemerida.....	1.0	9.0	0	2.0
Hyalella.....	1.0	11.0	0	1.0
Tabanidae.....	0	1.0	1.0	5.0

bottom samples as in plant samples; mayflies and scuds were nearly all collected by dredge sampling.

A comparison of the percentage composition by volume, which is believed to be a more reliable criterion of the potential fish-food supply than the percentage composition by numbers, gives a somewhat different picture. The libelluline dragonflies were more equally divided between plant and dredge samples than were the gomphine dragonflies, which bulked more than twice as large in the bottom samples as in the plant samples, a result that might be expected from the burrowing habit of this latter group. Damselflies, caddis, snails, and leeches all constituted a larger percentage (in most cases twice as large) of the plant fauna than of the bottom fauna. The proportionate volume of midges is about equal in plant and bottom samples. Mayflies and scuds were found almost entirely in the dredge samples, seldom occurring on the plants.

These data indicate that the picture of the species composition, volume, and number of fish-food organisms present in a lake obtained by dredge sampling is different from the picture obtained by plant sampling. Part of the explanation of the desirability of the two methods lies in the importance of the different groups of invertebrates as food for fishes. This phase has been considered under a later section.

It is believed that combining data concerning organisms from dredge samples and plant samples will give a more correct representation of the invertebrates in the lake than can be obtained by either sampling method alone.

BOTTOM FAUNA, 1940

As a result of the plant kill in the summer of 1940, all invertebrate sampling was done by dredge. During the period April 15-November 20, 1940, 377 dredge samples were taken. The invertebrates in these samples were tabulated by number, by volume, by percentage of the total number, and by percentage of the total volume. These tabulations, along with other pertinent data concerning the collections, are presented in Table 6.

As was true of the 1939 samples, aquatic insects were numerically and volumetrically the most prevalent of the invertebrates in the 1940 samples. The three groups of insects, the Odonata, Trichoptera, and midges, constituted approximately 60 percent of the num-

TABLE 6—*Invertebrate fauna collected by dredge sampling, 1940*

Collection dates.	April		May		June		July		August		September		October			
Number of samples.....	24		32		15		108		144		30		25		378 (total)	
Total area of samples (sq. ft.)..	7.5		8.0		7.78		30.46		36.0		7.5		6.25		103.50 (total)	
Total number of organisms.....	343		491		257		806		1064		310		1104		4375 (total)	
Number of organisms per sq. ft.....	46		61		33		26		30		41		176		42 (average)	
Total volume of organisms (cc.)..	9.96		10.45		7.23		24.88		31.66		10.87		18.73		113.78 (total)	
Volume of organisms per sq. ft.....	1.33		1.30		.93		.82		.88		1.45		3.00		1.10 (average)	
Libellulidae...A	23	6.71	39	7.95	6	2.33	55	6.83	68	6.80	20	6.45	32	2.90	243	5.55
B	1.27	12.71	2.23	22.30	.59	8.15	6.70	26.92	7.42	23.43	1.12	10.30	3.45	18.41	22.75	19.99
Gomphinae...A	25	7.30	15	3.05	27	10.50	93	11.50	125	11.74	30	9.67	40	3.62	355	8.11
B	2.44	24.42	.99	9.45	1.97	27.20	9.49	38.14	14.29	45.13	3.04	27.96	1.94	10.35	34.16	30.02
Aeschninae...A			1	.20			1	.12	4	.37					6	.14
B			.30	2.87			.11	.44	.75	2.36					1.16	1.01
Zygoptera...A	32	9.34	23	4.70	9	3.50	1	.12	13	1.22	18	5.80	130	11.75	226	5.17
B	.33	3.30	.36	3.43	.13	1.80	.01	.04	.18	.57	.13	1.19	1.04	5.55	2.18	1.91
Trichoptera...A	36	10.51	27	5.50	3	1.17	45	5.60	254	23.87	104	33.60	132	11.90	601	13.73
B	1.99	19.91	1.37	13.10	.05	.69	.84	3.37	3.89	12.28	2.51	23.08	5.34	28.51	15.99	14.05
Midges.....A	147	42.92	119	24.21	160	62.20	401	49.70	119	11.15	9	2.90	291	26.35	1246	28.48
B	.63	6.30	.50	4.78	.49	6.28	1.53	6.14	.43	1.36			1.22	6.51	4.80	4.21
Snails.....A	10	2.92	116	23.60	6	2.33	9	1.11	17	1.60	17	5.50	195	17.62	370	8.45
B	1.25	12.50	2.43	23.30	.73	10.10	.90	3.61	1.14	3.60	.88	8.09	4.15	22.15	11.48	10.08
Leeches.....A	2	.58	1	.20	2	.78	18	2.22	29	2.72	7	2.26	8	.72	67	1.53
B	.70	7.00	.01	.09	.05	.69	2.99	12.01	2.15	6.79	2.07	19.04	.72	3.84	8.69	7.63
Ephemeraidae...A	22	6.42	26	5.30	9	3.50	1	.12	3	.28			33	2.97	94	2.14
B	.03	.30	.13	1.24	.07	.97							.10	.53	.33	.29
Hyalella.....A	31	9.05	25	5.08	22	8.55	174	21.60	426	39.95	92	29.65	231	20.90	1001	22.88
B	.01	.10	.02	.19	.03	.41	.22	.84	.36	1.13	.05	.46	.06	.32	.75	.66
Gammarus...A	1	.29	2	.41							6	1.93			9	.21
B	.03	.30	.14	1.30							.04	.37			.21	.18
Tabanidae...A	4	1.17	3	.61	5	1.94	3	.36	5	.70	3	.97	2	.19	27	.62
B	.97	9.71	1.05	10.05	3.00	41.50	1.80	7.23	1.05	3.31	.99	9.10	.57	3.04	9.43	8.28
Coleoptera...A					5	1.94									5	.11
B					.09	1.24									.09	.08
Pisidium.....A	9	2.63	94	19.10			3	.36	1	.10	4	1.29	3	.27	114	2.60
B	.11	1.10	.92	8.80			.03	.12	.01	.03	.04	.37	.04	.21	1.15	1.01
Nepidae...A	1	.29														
B	.20	2.00													.20	.18
Other Diptera...A					3	1.17							4	.36	7	.16
B					.02	.28							.01	.05	.03	.03
Naucoridae...A							1	.12					1	.09	2	.05
B													.08	.43	.08	.07
Crayfish.....A																
B							.26	1.04							.26	.23

A=Number of organisms and percent of all organisms by number.

B=Volume of organisms in cubic centimeters and percent of all organisms by volume.

ber and 70 percent of the volume of all macroscopic invertebrates in the lake. The small scud, *Hyaletta*, ranked high in numerical importance but volumetrically was of little consequence as possible fish food. The snails were found in approximately the same proportion by volume as by number in bottom samples. The leeches and tabanid larvae were taken infrequently but because of their large size contributed an appreciable bulk to the total volume of organisms. Other organisms added little to the total volume or number of the aquatic invertebrates when considered on a seasonal average.

Figure 6 shows the percentage composition of invertebrates as determined by dredge sampling in 1940.

Figure 7 is a graphic representation of the abundance of invertebrates on the lake bottom during the summer of 1940. As indicated by the chart, the volume and number per square foot declined from an early spring high to a low point in July, following which there was a rapid increase in invertebrates throughout the summer.

BOTTOM FAUNA, 1941

During the period from April 1 to May 16, 1941, 80 dredge samples were collected in Third Sister Lake. These were taken before and a short time after the poisoning of the fish by rotenone which has been

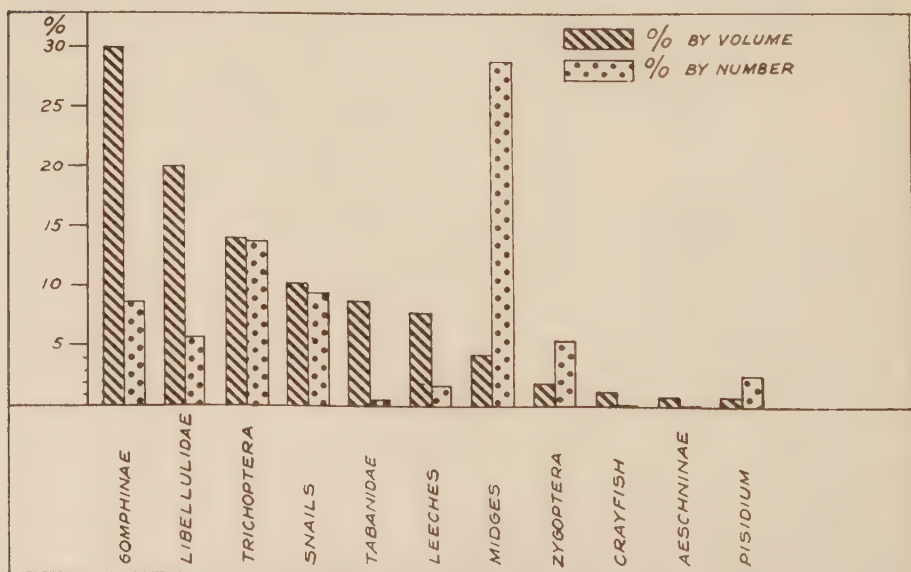


Fig. 6. Percentage composition of bottom fauna, 1940.

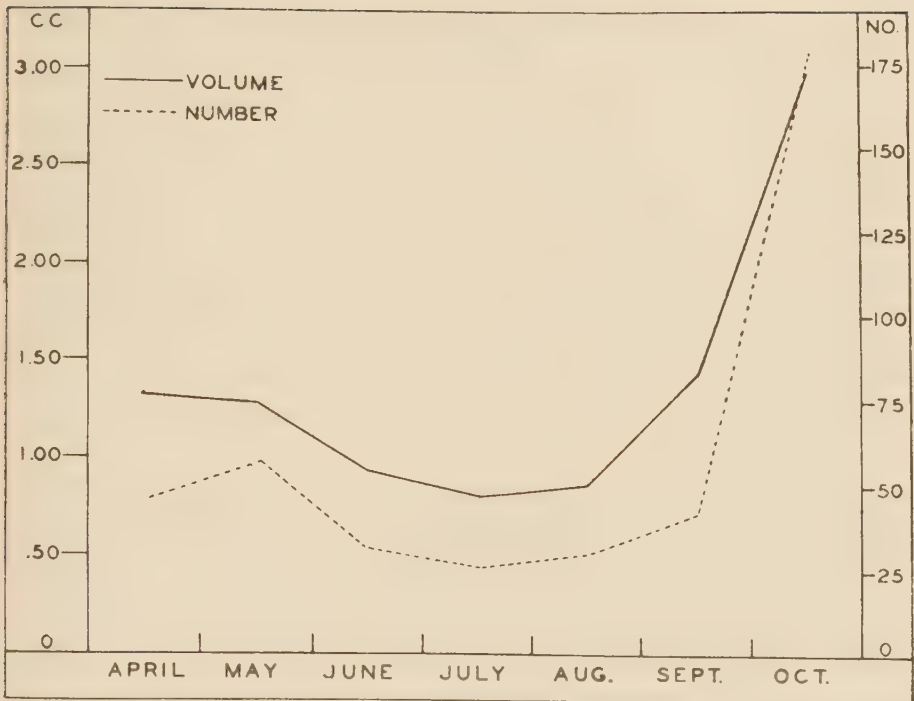


Fig. 7. Volume and number of invertebrates per square foot of lake bottom, 1940.

described by Brown and Ball (1942a). The poisoning of the fish occurred May 6, and the last dredge collection included in this series was made on May 16, 10 days later. It was shown by experiments carried out during the poisoning that the rotenone had no marked deleterious effect upon the macroscopic invertebrate fauna, (Brown and Ball, 1942b). The effects of the removal of the fish upon the invertebrates were studied for approximately a year following the poisoning and will be presented in a later paper. Data for 1941, shown in Table 7, are not strictly comparable with data for 1939 and 1940 for several reasons. First: the samples considered were obtained earlier in the year, beginning about the first of April, when the ice broke up on the lake, and ending May 16; thus they were in that period of the open-water season when the least data for the other two years are available for comparison. Second: during the period when these samples were collected, as many fish as possible were being removed by hook-and-line and nets for food samples and fish removal experiments. This removal undoubtedly lightened the predation pressure

of the fish on the invertebrates and may have been reflected in the number and volume of the invertebrates taken by sampling.

The 1941 sampling prior to poisoning was completed before the submerged aquatic vegetation had made an appreciable amount of growth, and therefore very little plant material was taken by dredge. Examinations of the plants early in the spring indicated clearly that the plants do not acquire their invertebrate fauna until they have reached a size and density that would afford some protection, nor until they have acquired at least a partial coating of periphyton. In Third Sister Lake the plants reach approximately half of their maximum individual size by the latter part of May, although the plant beds are more sparse than later in the summer when they have reached their growth peak.

The percentage composition of invertebrates in the samples is shown graphically in Fig. 8. Although the 1941 collections cannot be accurately compared with those of the preceding two years, it is of interest to note the similarities and differences in their composition. In these early-season samples, the immature dragonflies are the most important group, volumetrically, with the midge larvae ranking second.

In general, the majority of the bottom samples were made up of the same groups of invertebrates that composed them the two pre-

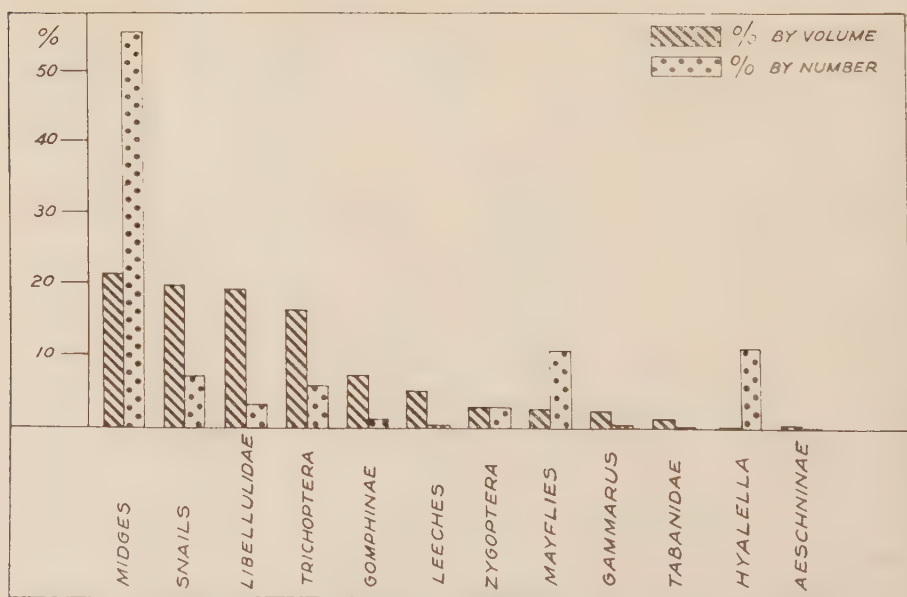


Fig. 8. Percentage composition of bottom fauna, 1941.

TABLE 7—*Invertebrate fauna collected by dredge sampling, 1941*

Collection dates.....	April 1, 1941	April 16, 1941	May 1, 1941	May 16, 1941	
Number of samples.....	22	24	28	6	80 (total)
Total area of samples (sq. ft.).....	5.5	6.0	7.0	1.5	20.0 (total)
Total number of organisms.....	1075	1467	1202	95	3839 (total)
Number of organisms per sq. ft.....	195	245	172	63	192 (average)
Total volume of organisms (cc.).....	14.86	18.55	17.03	1.43	51.87 (total)
Volume of organisms per sq. ft.....	2.70	3.03	2.43	.95	2.59 (average)
Libellulidae.....	A 35 3.28 B 1.73 11.64	47 3.20 3.39 18.27	56 4.66 4.27 25.06	7 7.35 .27 18.87	3.78 18.60
Gomphinae.....	A 23 2.14 B 1.70 11.44	18 1.23 1.82 9.81	9 .75 43 2.52		1.30 7.60
Aeschninae.....	A 1 .02 B .10 .67	1 .07 .08 .43			.05 .35
Zygoptera.....	A 29 2.70 B .28 1.88	39 2.66 .34 1.83	35 2.91 .74 4.34	2 2.10 .04 2.80	2.74 2.70
Trichoptera.....	A 89 8.28 B 2.93 19.71	79 5.07 2.94 15.85	61 5.07 2.78 16.32		5.96 16.65
Midges.....	A 755 70.22 B 4.68 31.50	795 54.22 4.37 23.55	502 41.76 1.95 11.44	69 72.45 .25 17.48	55.24 21.70
Snails.....	A 43 4.00 B 3.13 21.06	140 9.55 3.59 19.35	80 6.66 3.10 18.20	4 4.20 .34 23.77	6.95 19.60
Leeches.....	A 3 .28 B .12 .81	4 .27 .74 3.99	5 .42 1.58 9.27	1 1.05 30 20.97	.34 5.30
Ephemeridae.....	A 11 1.02 B .04 .26	159 10.84 .50 2.69	221 18.38 .69 4.05	1 1.05	10.20 2.37
Hyalella.....	A 84 7.81 B .02 .13	159 10.84 .05 .27	209 17.39 .12 .70	10 10.50 .01 .69	12.01 .25
Gammarus.....	A 1 .09 B .03 .20	6 .41 .48 2.59	7 .58 .60 3.52		.37 2.14
Tabanidae.....	A B	1 .07 .03 .02	3 .25 .60 3.52	1 1.05 .22 15.38	.13 1.64
Pisidium.....	A B	19 1.30 .22 1.18	3 .25 .03 .18		.57 .48
Other Diptera.....	A .01 .09 B .10 .67				.02 .02
Oligochaeta.....	A B		11 .92 .05 .29		.28 .01

A = Number of organisms and percent of all organisms by number.

B = Volume of organisms in cubic centimeters and percent of all organisms by volume.

ceeding years, although there was a change in the volumetric relationship. The midges show a greater volume in the samples for 1941 than for the other years, quite likely because of a seasonal reduction by emergence soon after this period. The early-season variation in volume is shown in Fig. 9.

SEASONAL VARIATION OF INVERTEBRATES

Nearly all the insects occurring in the bottom samples have a terrestrial phase in their life cycle, and when they enter this phase

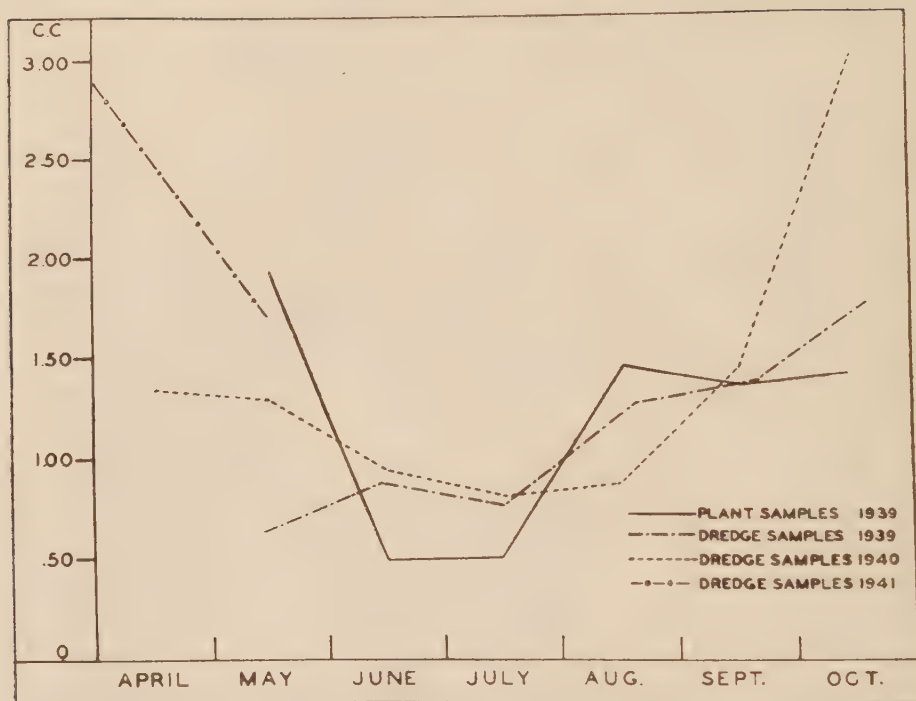


Fig. 9. Volumetric comparisons of invertebrate population for 1939, 1940, 1941.

it is reflected by fewer numbers of them in the bottom samples. Most of the other macroscopic invertebrates present in the lake occur in such small numbers that any decrease or increase in numbers could not be reliably interpreted from information gained by bottom sampling. One exception was the scud, *Gammarus fasciatus*. This amphipod was present each year during early spring, when the water of the lake was cold, and disappeared with increasing water temperature. *Gammarus* was not found in samples, or by intensive collecting with an aquatic dip net, after the water temperature reached 70° F., the critical temperature apparently being between 60° and 65° F. It reappeared in samples when the water temperature decreased in late September, was common in the lake during the latter part of October, and was collected by dredge sampling through the ice cover in winter. The small scud *Hyaella knickerbockeri*, was present the year around.

Pentland (1930) found a similar condition in southern Ontario waters, where specimens of *Gammarus fasciatus* were abundant until

March, when they began to decrease, and during the summer none were found. Pentland indicated that 54° F. was about the maximum temperature at which *Gammarus* are present.

COMPARISON OF INVERTEBRATE FAUNA FOR 1939, 1940, AND 1941

A comparison of the volume of invertebrates per unit area in the lake for the summers of 1939, 1940, and the collection period of 1941 is presented in Table 8. These data give a picture of the volume of invertebrates for each month of the collecting periods, and also the annual change in average total volume.

These data show that the summer average of invertebrate fauna per square foot as determined by bottom sampling did not vary greatly for the summers of 1939 and 1940, the variation being about 10 percent, which is within the error limits of the method. The actual variation in total macroscopic invertebrate fauna of the lake for the two years is not known, because the plant kill complicated the interpretation of data collected for the period. If the dredge samples only are compared, variation is slight, but if total volumes of plant and dredge samples for 1939 are compared with 1940 dredge samples, the variation is great and indicates a severe decline in volume of fish-food organisms in 1940, for which the plant kill may be responsible. As previously mentioned, a certain quantity (percentage unknown) of 1939 plant-dwelling invertebrates are included in dredge collections, which would increase the variation for the two years, but still, by any comparison, the average volume for 1940 was lower than for 1939. The volume of organisms per square foot of lake bottom for 1939,

TABLE 8—Comparison of volume of invertebrate organisms per unit as collected by plant and dredge sampling

Month	1939 Plant samples (cc. per pound)	1939 Dredge samples (cc. per sq. ft.)	1939 Plant + Dredge samples	1940 Dredge samples	1941 Dredge samples
April.....				1.32	3.04
May.....	1.02	.63	2.55	1.24	2.18
June.....	.50	.87	1.37	.81	
July.....	.51	.79	1.30	.82	
August.....	1.44	1.27	2.71	.86	
September.....	1.38	1.39	2.77	1.37	
October.....	1.42	1.75	3.17	2.95	
Average volume.....	1.25	1.24	2.49	1.10	

1940, the collection period of 1941, and the volume per pound of plants for 1939, are shown in Fig. 9. The general condition of an abundance of food in early and late summer months, with a period between having a greatly reduced invertebrate volume, is shown by this graph.

EFFECTS OF PLANT KILL ON INVERTEBRATES

An effort was made, with little success, to determine the qualitative effects of the plant kill on invertebrates. Without a more complete knowledge of species composition of invertebrate fauna, their normal habitat range, and normal population fluctuations than was obtained in this study, it was impossible to determine what changes were wrought.

The Trichoptera, which in this lake are known to be largely plant-inhabiting, comprised not nearly as great a percentage (by volume) of the bottom fauna in 1940 as in 1939, and gomphine dragonflies, known to be bottom-dwelling forms, constituted a much larger proportion. A reduction in the Zygoptera, which are chiefly found on plants, was noted.

It cannot be said that these changes are beyond normal fluctuations that may occur from year to year, but they are changes in groups of organisms that might be expected to be influenced by a plant kill such as took place in Third Sister Lake, and the change was in the direction that might be expected.

STUDY OF FEEDING HABITS OF FISH

METHODS

PROCEDURE FOR OBTAINING FISH

Third Sister Lake supported the predominantly bass-bluegill type of fish population so commonly encountered in the southern third of Michigan. For this reason, conclusions drawn from this study should be generally applicable to other lakes of this type. With this in mind, the food study was concentrated on bass and bluegills, with the latter species furnishing the majority of the data, although as far as possible all game and coarse fish were collected approximately in proportion to their relative abundance in the lake. A summary of numbers, weights, and pounds per acre of all fish recovered from Third Sister Lake at the time of poisoning are shown in Table 9.

TABLE 9—Summary of numbers, weights, and pounds per acre of all fish recovered from Third Sister Lake

Species*	Number	Percent of total number	Weight (pounds)	Percent of total weight (pounds)	Pounds per acre
GAME FISHES:					
Largemouth black bass.....	470	3.04	126.9	14.64	12.69
Bluegills.....	4,057	26.25	537.3	61.99	53.73
Pumpkinseed sunfish.....	610	4.07	29.2	3.37	2.92
Hybrid sunfish.....	13	0.08	2.2	0.25	0.22
COARSE FISHES:					
Green sunfish.....	96	0.62	5.4	0.62	0.54
Yellow bullhead.....	670	4.34	88.1	10.16	8.81
Common sucker.....	10	0.06	22.7	2.63	2.27
Chub-sucker.....	947	6.13	16.6	1.92	1.66
Mud pickerel.....	138	0.89	8.7	1.00	0.87
FORAGE FISHES:					
Black-chinned shiner.....	3,215	20.80	6.6	0.76	0.66
Black-nosed shiner.....	4,530	29.31	8.3	0.96	0.83
Common shiner.....	30	0.19	6.6	0.76	0.66
Golden shiner.....	174	1.13	5.9	0.68	0.59
Mud minnow.....	230	1.49	1.8	0.20	0.18
Iowa darter.....	264	1.71	0.3	0.04	0.03
Grand total.....	15,454		866.6		86.66

*The categories of game, coarse, and forage fishes are in accordance with the present legal classification in Michigan.

At the beginning of the investigation, it was planned to take with nets all fish to be used for food studies, as it was believed it would be possible to obtain enough fish for this purpose by trap and fyke nets and that netting would be less selective in its take of fish than other methods. It was soon discovered that nets would not consistently furnish enough fish for food studies and that they were quite selective in their catch. In addition, it was noted that less than 50 percent of the fish taken in the nets had any food in their stomachs and that much of the food present was digested to the extent that identification was difficult. When the traps were lifted at 30-minute intervals, 90 percent of the fish had identifiable food in their stomachs, but this method of obtaining fish for food studies was obviously not suited to an extensive program. Because any change in feeding habits of the fish which might result from a reduction of population was to be avoided, and because of other investigations being carried on at the same time, it was apparent that the trapping of fish would not be advisable.

Capture of fish by seines was not feasible in this lake because of the dense beds of submerged aquatic plants, the precipitous slopes and yielding bottom of the littoral zone, and the necessity for doing much of the work alone. Gill nets could not be used, as the fish re-

leased from them often do not survive and any unnecessary kill was to be avoided.

Following the trial with the nets, fish for food studies were taken with a fly or casting rod, using artificial lures. By this method it was usually possible to take all of the fish necessary for food samples in a short time, and over 95 percent of the bluegills had food in their stomachs.

All of the fish used in the food study were taken during the open-water period of the year. Attempts to take fish during periods of ice cover were unsuccessful in spite of repeated efforts with fyke nets, gill nets, and hook and line by several expert fishermen. An average of one game fish for each five hours of hook-and-line fishing was recorded for the three winters' work, which is considered very poor fishing for the lakes of this region. Fish taken through the ice were in exceptionally good condition, with much mesenteric fat.

With the exception of two bass, all game fish taken through the ice were bluegills, and their empty stomachs and intestines indicated that they had not fed for some time prior to capture. The stomachs of the two bass were removed 4 hours after capture. One of these was empty, and a live tadpole was found in the other.

It is believed that inability to take fish in winter on this lake does not in any way invalidate the conclusions drawn from food studies carried out only during the open-water period. Any change in the food supply during the winter would have little or no effect on the growth of game fish since the low temperature reduces their metabolism to a point where food taken during the period of ice cover would produce little or no growth.

Hathaway (1927) found that bluegills and largemouth bass consumed one-third as much food at 50° F. as at 68° F. Markus (1932), in studying the feeding habits, rate of digestion, and growth of largemouth bass at different temperatures during a 3-month period, concluded that the bass fed voluntarily at a temperature of 61° F. and above, and not at all at 50° and 39° F. Smith and Swingle (1940) stated that the growth of bluegills is retarded during the relatively mild winters of Alabama to a point that makes winter fertilization of ponds inadvisable. Leonard (1941) reported that digestion in living brook trout taken in the winter had nearly reached a standstill, as 3 hours after capture of the trout some food organisms were sufficiently vigorous to crawl from the stomachs of the trout, out through the

gullet and mouth, and creep about in the tray in which the trout were placed. He also reported soft-bodied, easily digested organisms having passed through the entire alimentary tract and being nearly intact near the vent.

PROCEDURE FOR ANALYZING

Largemouth bass, bluegills, pumpkinseeds, green sunfish, and common shiners were taken on fishing tackle from a boat. Bullheads were taken only by nets. The stomachs of the fish were removed and the contents preserved immediately following capture, as it was found that the food organisms were in much better condition for study if preserved immediately than if the fish were held, either dead or alive, even for a short time.

Thirty minutes' exposure to the high temperatures of surface water in the bottom of a boat during midsummer so increased digestive action that stomach contents were, in most cases, useless for food studies. As soon as a fish was captured, it was weighed, measured, and sexed. Scale samples were taken, and the stomach contents were removed and preserved in alcohol. The measurement of stomach samples was carried out in a manner similar to that of the invertebrates taken in bottom and plant samples. Identification, numerical counts, and volumetric measurements were made of organisms from the stomachs.

FEEDING HABITS OF FISHES

LARGEMOUTH BASS

During the course of the investigation, 63 bass were collected for food studies; of these, 41 had food in their stomachs. The bass ranged in size from 8.2 to 16.8 inches, with the average being 10.3 inches. Data concerning the stomach contents of these fish are presented in Table 10 and indicate that frogs, crayfish, and fish are the important items in the diet of bass. The presence of many crayfish in the stomachs of the bass was an unexpected discovery, since crayfish were seldom taken in bottom samples or seen in shallow areas of the lake. Bluegills formed a staple portion of the bass diet in all collection periods, although their importance as food, as indicated by their percent by volume, is somewhat distorted by the large size of the frogs captured, which lowered the relative percentages of other foods. The proportion of insects in the diet of the bass might have appeared greater if more fish in the smaller size groups had been taken, but

from observations the bass were seen to take young sunfishes as soon as the two species were large enough to be identified by the observer from a boat.

PUMPKINSEEDS

Thirty-three pumpkinseeds were included in the food studies. These fish ranged from 5.5 to 7.3 inches in total length with an average size of 6.3 inches. The results of this study definitely establish this species as a mollusk eater in this lake, a food preference made possible by its possession of heavily paved pharyngeal teeth. This food preference is in accordance with the findings of others, notably Baker (1916), who found that between 60 and 70 percent of the food of this species in Oneida Lake, New York, consisted of snails. For the pumpkinseeds studied, snails constituted approximately 83 percent of all food by number and 67 percent by volume. Dragonfly nymphs were second

TABLE 10—Food of largemouth bass, pumpkinseeds, and bullheads in Third Sister Lake

Fish foods	Largemouth bass		Pumpkinseed		Bullhead	
	Percent by number	Percent by volume	Percent by number	Percent by volume	Percent by number	Percent by volume
FROGS						
Adult.....	8.63	69.00			.22	3.60
Tadpole.....	2.16	4.60				
FISH						
Bluegills.....	23.00	5.10			2.63	39.60
Chub suckers.....					.66	8.02
Minnows.....	15.80	2.24				
Darters.....	6.46	1.21				
MOLLUSCA						
Snails.....			82.80	67.50	1.09	.35
ARTHROPODA						
Grustacea						
Gammarus.....					59.60	.32
Crayfish.....	4.30	13.25			1.31	11.30
Insects						
Libellulidae.....	8.65	.96	1.42	8.10	5.05	2.81
Aeschninae.....					1.31	.19
Gomphinae.....	3.60	.57	1.13	11.95	4.16	2.56
Zygoptera.....	2.16	.10	.57	.55	.22	
Trichoptera.....	.70	.04	.71	1.41	.66	
Notonectidae.....	1.44	.25				
Naucoridae.....	1.44	.16				
Nepidae.....	.70	.13				
Dytiscidae.....	.70	1.51				
Ephemera.....					.88	
Midges.....	18.70	.09	8.10	1.33	17.80	.82
Tabanidae.....	.70	.13	.14	3.29	.66	.70
ANNELIDA						
Leeches.....	.70	.06	.14	2.66	3.28	9.39
Earthworms.....				2.82		18.70
SPONGE.....		.45				
PLANTS.....				.47		.20

in importance as food. This study indicates that the pumpkinseed has a decided predilection for snails and chooses them from among the other foods present. Pumpkinseeds were taken in the same area, at the same time, and by the same methods as were bluegills, but comparison between these individuals showed no similarity of feeding habits. Data compiled from the study of the food of pumpkinseeds is presented in Table 10.

YELLOW BULLHEADS

Approximately 50 percent of the bullheads collected for food studies had no identifiable food in their stomachs owing to the fact that all fish were taken in nets and many were held long enough to digest the food taken before being trapped, while others regurgitated their food upon being lifted from the water. These fish ranged in size from 7.1 to 13.2 inches total length, with an average length of 10.6 inches. This food study indicated that the yellow bullheads were omnivorous in their feeding habits, and of the aquatic organisms utilized as food, fish and crayfish were taken in greatest volume.

BLUEGILLS

Six hundred and fifty-two bluegills were taken for food studies. Of these, 64 were not included in the final tabulation for one of several reasons. In the capture of bluegills with hook and line, the smallest size group was not included. These were in Age Group I and

TABLE 11—Age, size, number and weight of bluegills recovered from Third Sister Lake*

Age group	Number of specimens aged	Size range total length (inches)	Average total length (inches)	Number	Percent of total number	Average weight (ounces)	Total weight (pounds)	Percent of total weight
I	28	1.1-1.8	1.4	1345	33.2	0.03	2.45	0.5
II	107	2.5-4.4	3.4	915	22.6	0.32	18.16	3.4
III	59	4.4-6.9	5.2	237	5.8	1.14	16.94	3.2
IV	72	4.7-7.3	6.5	280	6.9	2.87	50.23	9.3
V	63	6.1-8.4	7.4	296	7.4	4.20	77.79	14.5
VI	68	6.8-8.7	8.0	360	8.9	5.38	120.97	22.5
VII	63	7.6-9.0	8.3	270	6.7	5.99	101.00	18.8
VIII	49	6.6-9.1	8.6	166	4.1	6.46	66.99	12.5
IX	17	8.2-9.3	8.7	108	2.7	6.79	49.85	8.5
X and over	4	8.1-9.6	9.0	80	2.0	7.39	26.93	6.9
Grand total				4057			537.30	

*Data from Brown & Ball (1942a).

part of Age Group II, as shown in Table 11. The number of fish included in this group is large, but their weight represents only 4 percent of the total and it has been assumed that their demand on the food supply is approximately proportional.

The age groups represented in this study included more than 95 percent of the weight of all bluegills as determined at the time of poisoning.

The length, weight, and sex, for the 583 (90 percent) fish used in the food study are shown in Table 12. In this table is shown an increase in the average weight and length of the fish for each successive year. The apparent increase in average length and weight may have been due to a lessening of competition for food because of the removal of 31 pounds of bluegills in 1939 and 62 pounds in 1940.

From a study of the scales of the fish taken at the time of poisoning, it was not possible to establish that there had been a definite increase in growth rate during these years above what might be encountered in the normal growth fluctuation of this species.

Beckman (1940) found that the removal of part of a stunted fish population in Standard Lake, Michigan, resulted in marked growth increase. While Third Sister Lake did not have a stunted fish population, it was believed that, for the existing species composition, it was producing the maximum weight of fish possible for the food supply, and therefore any reduction of pressure on the food supply might result in increased growth.

The sex ratio was approximately 9 males to 10 females. This coincides closely with the figures given by Beckman (unpublished) for bluegills of the same age groups from Michigan lakes.

The coefficients of condition for the different groups of bluegills are somewhat lower than those recorded by Bennett, Thompson, and

TABLE 12—Data concerning bluegills used in food study

	1939	1940	1941	Totals and averages
Number of fish.....	152	279	157	588
Weight range (gm.).....	22-240	24-246	23-258	
Average weight (gm.).....	94	101	135	110
Length range (mm.).....	111-250	111-234	102-250	
Average length (mm.).....	170	175	198	181
Number of males.....	73	125	68	266
Number of females.....	79	154	89	322
Total weight (pounds).....	31.52	62.25	46.60	140.37

Parr (1940) for Fork Lake, Illinois, a test lake from which fish were removed at the rate of 25 pounds per acre per month during the growing season (6 months).

As has been discussed in a previous section, the dominant species of the submerged aquatic plants, *P. amplifolius*, was abundant during the summer of 1939 and almost completely killed in the summer of 1940. Several changes in feeding habits of the bluegills that could well be attributed to this ecological change were noted in the 1940 stomach analyses. A general trend, almost without exception, toward lower numbers and smaller volume of the macroscopic aquatic invertebrates, appeared in the food samples of 1940. This reduction was accompanied by an increase in the number and volume of terrestrial insects and plankton organisms taken as food during the same period. One change that seemed due to the plant kill was shown by a member of the family Ephydriidae (Diptera), *Hydrellia*, a small black fly whose larval life is spent in the tissues of some of the potatoetons of this lake. The adult of this fly was common around the lake during the summer of 1939 and composed 6 percent of the number and 2 percent of the volume of all foods taken by bluegills. The following summer, when the plants were absent, no record was made of its occurrence in the food of the fishes.

Snails taken as food were nearly all small individuals, mostly *Gyraulus* or *Amnicola*.

The terrestrial insects considered in the food study are those that do not pass any phase of their life cycle in the lake. Also included with these were *Syrphus* flies, Dolichopodidae, Empidae, and other families of the Diptera that include some genera or species having an aquatic phase in their life cycle. It is difficult and time-consuming to determine species of these groups from fragments and broken individuals found in bluegill stomachs, and species identification is necessary in most cases to determine whether there is an aquatic phase in the life cycle. Very little error was introduced by including the few doubtful groups with the terrestrial insects, as the volume or number of these taken by fish was not large. The terrestrial insects most commonly found in the bluegill stomachs were those living around the lake shore, although at certain times during the summer months large numbers of winged ants floated on the surface of the lake, and the fish fed extensively on them. As these periods were of short duration, they did not influence the total summer food volume to an appreciable extent.

Included under the heading of plants taken as food are both aquatic vascular plants and algae. Only about 2 percent of the plant material was algae, the remainder being mostly *Najas gracillima*, and occasionally leaves of narrow-leaved *Potamogeton zosteriformis*. An effort was made to determine whether the plants found in the stomachs were taken as a primary source of food or incidentally to the capture of the invertebrates that live on and among the plants. The evidence pointed to the plants being taken as food and not incidentally. In the great majority of cases when the stomach contained *Najas* there was no other food present, and the individual leaves were nearly of the same length, as if they had been cropped off intentionally, rather than of all lengths as would seem probable if taken in a lunge at an intended prey.

Table 13 shows the percentage composition by number and by

TABLE 13—Food of bluegills in Third Sister Lake

	1939		1940		1941	
	Percent by number	Percent by volume	Percent by number	Percent by volume	Percent by number	Percent by volume
FISH FRY.....	---	---	.48	.19	---	---
FISH EGGS.....	---	---	1.10	.55	---	---
MOLLUSCA						
Snails.....	6.05	1.55	1.81	1.13	1.33	2.46
Pisidium.....	+	+	+	+	+	+
ARTHROPODA						
Gammarus.....	+	+	+	+	+	+
Hyaella.....	+	+	+	+	+	+
Hydracarina.....	+	+	+	+	+	+
AQUATIC INSECTS						
Libellulidae.....	5.51	10.04	.56	4.35	.69	8.42
Aeschninae.....	.20	5.22	.14	1.10	.03	.72
Gomphinae.....	.41	3.46	.26	2.06	.52	7.62
Zygoptera.....	4.93	1.55	.69	1.58	.85	1.37
Trichoptera.....	5.83	4.33	3.52	2.76	.43	1.37
Midges.....	54.69	14.66	37.00	14.50	90.48	45.67
Ephemera.....	+	+	+	+	+	+
Corixidae.....	1.25	1.70	.25	2.05	+	+
Notonectidae.....	+	+	+	+	+	+
Halipidae.....	+	+	+	+	+	+
Hydrellia.....	5.63	1.71	---	---	.93	.12
Dytiscidae.....	+	+	+	+	+	+
Donacea.....	+	+	+	+	+	+
Coleoptera.....	+	+	+	+	+	+
Gyrinidae.....	+	+	+	+	+	+
Nymphula.....	+	+	+	+	+	+
Tabanidae.....	+	+	+	+	+	+
Naucoridae.....	+	+	+	+	+	+
Sialidae.....	+	+	+	+	+	+
Hydrometridae.....	+	+	+	+	+	+
LEECHES.....	+	+	+	+	+	+
PLANTS.....	---	20.57	---	18.50	---	10.25
SPONGE.....	---	---	---	1.24	---	2.63
INORGANIC DEBRIS.....	---	3.18	---	1.27	---	4.58
ORGANIC DEBRIS.....	---	3.38	---	2.54	---	7.16
ZOOPLANKTON.....	---	9.57	---	24.00	---	1.74
TERRESTRIAL INSECTS.....	12.19	15.23	50.00	20.30	.52	2.86

--- = Not present.

— = Not considered numerically.

+ = Present but less than 1 percent.

volume of the food of bluegills for 1939, 1940, and 1941. The absence of fish eggs in the stomach-analysis tabulation can be explained by the fact that there were few small fish collected of the size so often seen around fish nests waiting to dart in and grab an egg when the guarding fish is away. The very few fish fry in the stomachs can be accounted for as selectivity on the part of the larger bluegills, as very few fry were taken although at times the entire shoal area seemed to be teeming with young-of-the-year fish. The few fish eaten by bluegills were nearly all minnow fry, probably either black-chin or black-nose shiners, which were very abundant in the lake.

In the original tabulation of the food of the bluegills the several size groups were considered separately, but as no food differences that could be ascribed to differences of size of the fish were found, all sizes were grouped together in the final analysis.

An unusual feature of the food study was the finding of fresh-water sponge gemmules in the stomachs of several fish. The fish were not all from one area and were taken in several different collections. There was no evidence from the stomach contents that the fish had eaten a mature sponge, as no sponge body spicules could be found and in most cases there was no other food in the stomachs containing this material. The gemmules were eaten in early spring.

Under the heading of inorganic debris is included all material whose source was doubtful or of inorganic origin. Under organic debris was included material of animal origin whose exact identification was not feasible.

The volume and number of zooplankters taken by the fish was much greater in 1940 than in 1939. Zooplankton organisms were not included in the calculations of the percentage composition by number, as such an inclusion would mean the complete numerical domination by them and give an undesired interpretation of the proportions of food organisms. Zooplankton was included in the percentage composition by volume of all foods.

No evidence was found that phytoplankton was being used as food by bluegills.

Computed on the basis of all foods eaten in the summers of 1939 and 1940, the following types were utilized by bluegills in the proportions shown on page 42.

	Percent by volume	Percent by number
Aquatic insects	43.0	78.0
Plants	21.0	—
Terrestrial insects	15.0	12.0
Plankton	10.0	—

Pearse (1918) found that bluegills in Wisconsin lakes during 1914 and 1915 fed mostly on insects (46 percent) and entomostracans (25 percent).

In a food study of 100 bluegills from Reelfoot Lake, Tennessee, McCormick (1940) stated that bluegills had eaten 52 percent by volume of plant material (*Ceratophyllum*), 34 percent chironomid larvae, and 13 percent other animal forms.

Moffett and Hunt (1943), in a winter fish-food study, found that bluegills of Cedar Lake, Michigan, were taking small fish, although infrequently. This was not found to be true in Third Sister Lake during the summer months. Moffett and Hunt also noted that there is little variation in the dietary constituents of different size groups of bluegills, which was true of the fish studied in this investigation. They found that the largest fish (200 mm.) tend to discontinue plankton feeding and turn to other foods, a change in feeding habits which was not true in this study, as the largest fish had been feeding on plankton.

Not a single *Corethra* was found in the bluegill stomachs examined, although these organisms were frequent in plankton samples from the upper 20 feet of water, and occasionally were seen emerging when fish were being collected. Howell (1941) found this true in his work with bluegills in Alabama ponds.

Howell, Swingle, and Smith (1941) recorded midge larvae and pupae as the most important bluegill food for fish over 1 ounce in weight. The next most common food was the dragonfly.

Bennett, Thompson, and Parr (1940), from a food study of bluegills in Fork Lake, Illinois, concluded that the most important groups of aquatic insects were Diptera, Odonata, and Hemiptera and of these, Diptera were consistently important. Although Hemiptera were common in Third Sister Lake, they were seldom taken as food by bluegills.

The insects listed in Table 13 as aquatic are those that spend at least part of their life cycle in the lake, even though they were taken

as adults from the surface of the water. In the final tabulation of analyses of food of bluegills collected during the summers of 1939, 1940, and 1941, no distinction was made between larval, pupal, and adult insects.

FORAGE RATIOS

In the past, most estimates of the capacity of bodies of water to support fish have been based on determinations of total bottom fauna, and arbitrary standards have been established by which a body of water could be classified according to the number or volume of animals occurring on an average square foot of bottom. The "food grade," established by Davis (1938), has been widely used in stream investigations. This evaluation of waters is based on the assumption that all types of animals in the bottom fauna are available and utilized in proportion to their abundance, but comparison between bottom organisms actually eaten by fish and bottom fauna present in the lake shows that there is great variation in the relative extent to which different animals are utilized as food. Muttkowski (1918) indicated that different food items in Lake Mendota did not form the same percent of fish food that they made up of the invertebrate fauna of the lake. Surber (1930) recognized the need for determining the relationship between the food of fish and the available or potential food supply of the same waters in his study of the upper Mississippi sloughs. Pate (1934), in a study of the Raquette Watershed of New York, made comparisons of the percent of food consumed by several species of stream fish with that present and available on the stream bottom. Hess and Swartz (1940) in their work on black-nose dace in Cascadilla Creek, N. Y., proposed the term "forage ratio" for the ratio of the percent which a given kind of organism constitutes of the total stomach contents to the percent which this same organism constitutes of the total population of food organisms in the fishes' environment.

Allen (1941) referred to this ratio as an "availability factor". To date, most investigations of this type have been on cold-water species of fish. Cooper (1941) reported on the summer diet of White Perch in 42 Maine lakes and ponds and correlated it with bottom fauna from these same waters.

The term "forage ratio" has been used in this investigation to describe the relationship between invertebrate fauna of Third Sister Lake and invertebrates of this fauna taken as food by bluegills.

A summary of the total food utilized by bluegills of Third Sister Lake, including plant material and terrestrial insects, has been presented, but to determine forage ratios for bluegills it has been necessary to recalculate the fish-food data to include only foods that can be obtained quantitatively by sampling.

For this reason terrestrial insects and plants were eliminated from calculations of food taken by bluegills, and the percent of each food item was computed on a basis of those fish-foods which can be collected quantitatively.

Data used here are from stomach analyses of bluegills collected during the summers of 1939, 1940, and the early part of 1941, and from bottom samples secured during the same periods.

The use of both number and volume of organisms must be considered when evaluating selectivity on the part of the fish, or availability of the organisms to the fish. Volume measurement is perhaps a better index to the benefit a fish receives from food organisms and number measurement presumably a better index of amount of effort in selecting and capturing its food.

In Table 14 is a summary of the percentage composition by volume, number, and forage ratios for five groups of organisms found to be important aquatic fish-foods in 1939, 1940, and 1941. The percentage values for the volume and number of organisms both in bottom samples and stomach samples have been recorded in whole numbers except where their value is less than 1. This will facilitate comparison of the different figures and is still within the limits of the error of the

TABLE 14—Comparison of percentage composition in bluegill stomachs, in invertebrate collection samples, and forage ratios for five aquatic fish-food organisms

	Dragonflies		Midges		Caddis		Damselflies		Snails	
	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.
1939										
Percent in samples.....	36	8	4	23	39	33	4	10	5	8
Percent in stomachs.....	36	3	34	73	11	9	3	2	2	3
Forage ratio.....	1	4	8	3	.3	.3	.6	.2	.5	.4
1940										
Percent in samples.....	51	14	4	29	14	14	2	5	10	9
Percent in stomachs.....	24	2	47	79	9	8	5	2	4	4
Forage ratio.....	.5	.2	11	3	.6	.6	3	.4	.4	.4
1941										
Percent in samples.....	29	4	24	54	16	5	2	3	19	10
Percent in stomachs.....	23	1	65	91	2	.4	2	.9	3	1
Forage ratio.....	.8	.3	3	2	.1	.1	1	.3	.2	.1

method. From this table it can be seen that of these organisms only the midges occurred in the diet of bluegills in a proportion greater than they occurred in the lake, that the forage ratios vary somewhat from year to year, and that forage ratios calculated on a volumetric basis are quite different from those computed on a numerical basis.

Allen (1941) stated that "values for availability factors (forage ratios) obtained from numerical results will differ slightly from those obtained volumetrically or gravimetrically. . . . It is doubtful, however, whether these differences are of great extent, and it is therefore probably satisfactory, if desired, to apply availability factors obtained on a numerical basis to volumetric or gravimetric measurements of faunistic density."

Data obtained in this study indicate that this conversion cannot be made.

SEASONAL RELATIONSHIP OF PLANT FOODS TO INVERTEBRATE FOODS

For a fuller understanding of the feeding habits of the bluegill, an effort was made to determine the effect of reduction of aquatic invertebrates, which normally takes place during part of each summer, upon the diet of the fish.

Sampling during the two summers showed that aquatic invertebrates, which constitute a large part of the summer food of bluegills, undergo a drastic reduction in numbers and volume during midsummer.

From the food study it was found that the percentage of plant food in the total volume of food in 1940 was as follows:

Date:	April	May	June	July	August	September	October	November
Percent	0.0	2	9	36	26	11.0	10	0.0

These data compared with data on invertebrate fauna as shown graphically in Fig. 10 indicate that plant food was eaten in an inverse ratio to the volume of invertebrates present in the lake during different periods of the summer. This same condition was found to be true in 1939. The inference to be drawn from this is that, when the animal food supply diminishes, bluegills turn to plant food as a substitute. *Najas gracillima*, which was the dominant plant food, was present throughout the summer period, and it seems unlikely that abundance had any effect upon the utilization of this plant as food.

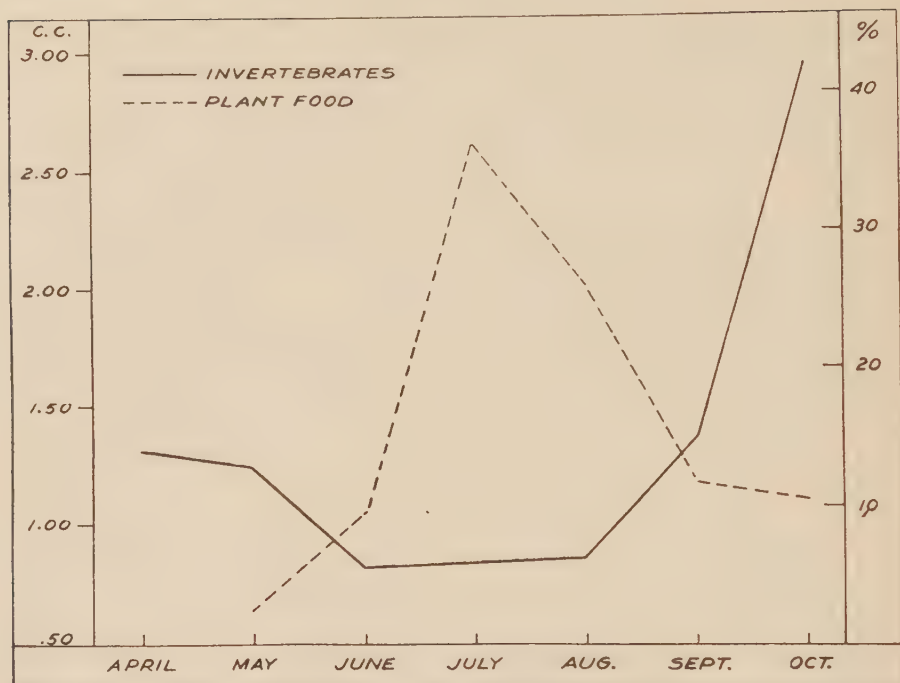


Fig. 10. Comparison of the volume of plants taken as food with the volume of invertebrates in the lake, 1940.

Howell, Swingle, and Smith (1941) concluded from work on bass and bluegill food in Alabama waters that, although bluegills do eat plant foods, animal foods are preferred, especially insects, and when large quantities of plant foods are being consumed it indicates that there are too many fish in the pond or lake competing for the same animal foods. Bennett, Thompson, and Parr (1940), in their food study of bluegills in Fork Lake, Illinois, found the fish to have eaten a considerable amount of coarse aquatic plants, and from their tables it can be seen that plants are present in increasing volume in the diet of the fish from April to July, then gradually decline. They interpret a higher percentage of plants eaten by older bluegills to mean that old fish are less active than yearling fish in seeking animal foods and that they use plants as "stuffing".

RELATIONSHIP BETWEEN COEFFICIENT OF CONDITION OF BLUEGILLS AND PLANT FOODS CONSUMED

It was believed that an increase in plant food in the diet might be reflected in the condition of the fish. To check this assumption, the

weight and length of fish used for food studies were tabulated and from these data the condition factor "C" was calculated for each month of the summers of 1939 and 1940, and for 1941 prior to poisoning. There is an indication of lowered coefficient of condition during August of each summer, but there is enough variation in the data of other months to cast some doubt as to whether this is a true reduction in the plumpness of fish attributable to a change in diet.

SEASONAL RELATIONSHIP OF INVERTEBRATE FOODS TO TERRESTRIAL INSECTS

An attempt was made to determine whether a correlation existed between seasonal variation of aquatic invertebrates and number of terrestrial insects taken as food. This material was summarized for the summers of 1939 and 1940, but so far as could be determined there was no correlation between scarcity of aquatic invertebrates and utilization of terrestrial insects by the fish. The terrestrial insects were apparently taken whenever available.

IMPORTANCE OF PLANKTON IN FISH DIET

Plankton samples were collected at the same time as were the temperature and chemical data. These collections were made with a Juday plankton trap of 10 liters capacity, at intervals of 10 feet, from surface to bottom. The plankton was preserved in formalin and identified at a later date.

Although zooplankton organisms were a considerable item in the food of fishes, phytoplankton was not found in the food of the bluegills studied. For this reason, only the zooplankton has been tabulated and considered in this investigation. In the fish-food study it was not possible, owing to time limitation, to divide up the zooplankters into taxonomic groups, and therefore they were counted and volumetrically measured as a whole. The zooplankters which constituted the bulk of the plankton fish food in the lake were *Epishura*, *Daphnia*, *Ceriodaphnia*, *Diaptomus*, and *Cyclops*.

FORAGE RATIOS FOR PLANKTON

A comparison of zooplankton organisms from the upper 20 feet of Third Sister Lake with the mean number of zooplankters per bluegill stomach collected during the same periods is made in Table 15. This limitation of depth was placed to make the material as compar-

TABLE 15—*Comparison of number of zooplankton organisms in the upper 20 feet of Third Sister Lake with mean number of zooplankters eaten by bluegills during the same period*

	Apr.	May	June	July	Aug.	Sept.	Oct.	Averages
1939								
Number per liter	504	236	73	70	155	203		206
Mean number per fish stomach		75	158	14	332	320	230	180
Forage ratio		.32	2.16	.20	2.14	1.57		
1940								
Number per liter		1881	732	873	939	725		1030
Mean number per fish stomach		1697	1450	501	465	585	1400	1016
Forage ratio		.90	1.98	.57	.50	.80		
1941								
Number per liter	895							
Mean number per fish stomach	111							
Forage ratio	.12							

able as possible to the feeding of the bluegills, which was confined to an area above this depth throughout most of the summer. The rapidity with which a plankton population can change in a lake and the relatively long period between these plankton collections, in most cases 2 weeks, make specific deductions unreliable, but the data show several general tendencies. In 1939, the plankton counts followed closely the curve shown in Fig. 2 representing the volume of invertebrate fauna for the same year, showing the low point of the summer during July and an increase from this point throughout the summer. The 1940 counts show somewhat the same tendency as that shown by the bottom fauna, in that there is an early spring abundance preceding a low point in early summer, followed by an increase during the ensuing months, although there is a drop in numbers of plankters in September. One change that does stand out is the difference in total numbers for the two years. The samples for 1939 averaged approximately 200 organisms per liter, while the 1940 collections averaged more than 1,000 per liter. A forage ratio was determined for plankton for the lake in relation to plankton eaten for each month of the two summers, and the results are shown in the Table 15. From these data, there is no evidence that fish fed more extensively on zooplankton during periods of abundance. Also there is no evidence that fish turn to this source of food when the invertebrate food produced in a lake is at a minimum.

It was noted that fish feeding on plankton were taking it almost to the exclusion of other foods.

DISCUSSION

The methods proposed by Davis (1938) for estimating the "food grade" of streams have been used extensively in determining policies for stocking streams. Statistical analyses of this method and modifications of it have been suggested by various workers (Hess and Swartz, 1940), (Allen, 1941), (Mottley, Rayner, and Rainwater, 1938), but little has been offered in the determination of food grade of lakes. Davis cites the fact that there have been relatively few quantitative studies of the bottom fauna of lakes as a handicap in evaluating lakes for purposes of fish management. He uses the classification of oligotrophic, eutrophic, and dystrophic, proposed by Thienemann and Nauman, to formulate a stocking policy for trout on the basis of whether the food supply of these types of lakes is average, abundant, or poor, respectively.

From the investigation of invertebrate fish food in 1939 and 1940, it can be seen that the application of any "food grade" standard would have little meaning when applied to Third Sister Lake, and presumably to other similar lakes, unless seasonal variations of invertebrate fauna were taken into consideration. The sampling of bottom fauna showed that there was a 274 percent fluctuation in volume of invertebrates per unit area of lake bottom during the summer of 1940.

Miller (1938, unpublished) offers a statistical analysis of lake-bottom fauna based on organisms inhabiting the profundal zone, which have a more random distribution than littoral fauna.

As far as is known to the writer, no adequate statistical analyses have been made of invertebrate sampling in the littoral zone. Deevey and Bishop (1941), in their work on Connecticut lakes, dealt statistically with bottom fauna collected mainly in the region below 3 meters in cold-water lakes. They stated, "bottom sampling in the littoral zone is unreliable at best, and probably no wholly satisfactory estimates have ever been made of the productivity of this region."

To better establish the position of Third Sister Lake as a producer of invertebrate fish food in comparison with other inland lakes that have been investigated on a similar basis, the results of several workers in different parts of the country have been tabulated in Table 16. This material from many sources has been rearranged and certain elements deleted in summarizing it so the results of the several workers are comparable. In some cases, the material was originally de-

terminated in units other than those given in the table, such as pounds per acre, grams per square meter, etc. These were all converted into their equivalent in cc. per square foot for purposes of this comparison. Whenever possible, only that material indicated by the author as having been collected in the littoral zone was used. If possible the mollusks were excluded from the tabulations. This was done in the data of Richardson (1921) and of Scott, Hile and Spieth (1928), where the molluscan element was large. Little in the way of specific comparisons of the results of these workers can be made, but some general conclusions can be drawn.

Lakes studied by Cooper (1939, 1940, 1941, 1942) were very poor in invertebrate fauna compared with other waters, such as lakes of the Illinois river bottom. In making such a comparison, the zones sampled must be considered, which in these cases were entirely different. Cooper collected nearly all bottom samples below a depth of 6 feet, and Richardson collected nearly all above 10 feet.

There are also many obstacles to any comparison between trout lakes and warm-water lakes. Cooper (1939) considered two Maine lakes having a bottom fauna of 0.14 and 0.17 cc. per square foot as being good trout lakes and two lakes having 0.08 and 0.004 cc. per square foot as being good salmon lakes. These figures were for samples taken below 5 feet, as he believed food organisms above that depth are not available to trout during much of the summer. Deevey and Bishop (1941) state, "It is also true that lakes of low potential productivity do not necessarily provide poor fishing. Low potential productivity is, in fact, one of the potential characteristics of most trout lakes." They believed that the excellent fishing in many Connecticut lakes in this category is perhaps due to the fact that the available food is efficiently used by an association of suitable game and forage species. As can be seen from Table 16, on the basis of bottom fauna Third Sister Lake is between the low productivity of the trout lakes and high productivity of the Illinois river-bottom lakes. In studies of bottom organisms in lakes, there has been little work done on the relationship between bottom organisms and the actual production of fish in the same bodies of water. Meehan (1936), in studies concerning the effects of fertilizing fish ponds, found that his ponds produced an average of 0.95 gram of invertebrate organisms per square foot of bottom and an average of 96.53 pounds of bass per acre. In addition to this, the ponds produced an unstated weight of forage fish. Howell (1941) attempted to show the relationship be-

TABLE 16—Data concerning bottom fauna compiled from published sources

Investigator	Date	Region	Depth of samples	Volume of samples (cc. per sq. ft.)
Cooper.....	1939	Maine.....	All.....	14-17 (1)
Cooper.....	1939	Maine.....	All.....	1.02 (2)
Cooper.....	1939	Maine.....	All.....	.08-.004 (3)
Cooper.....	1940	Maine.....	All.....	.092
Cooper.....	1941	Maine.....	All.....	.34
Cooper.....	1942	Maine.....	All.....	.28
Deevey and Bishop.....	1941	Connecticut.....	All.....	.77
Townes.....	1938	New York.....	0-12 feet.....	3.73
Nevin.....	1936	New York.....	0-10 feet.....	2.63 (collected in early July) (4)
Nevin.....	1936	New York.....	0-10 feet.....	.78 (collected in August) (4)
Nevin.....	1936	New York.....	0-10 feet.....	2.32 (collected in June-July) (5)
Nevin.....	1936	New York.....	0-10 feet.....	3.14 (collected in late August) (5)
Burdick.....	1940	New York.....	All.....	1.46
Scott, Hile, & Spieth.....	1928	Indiana.....	Littoral zone.....	1.44
Richardson.....	1921	Illinois.....	Littoral zone.....	1.66 (weedless areas) (6)
Richardson.....	1921	Illinois.....	Littoral zone.....	4.59 (weed beds) (6)
Richardson.....	1921	Illinois.....	Littoral zone.....	8.53 (weed samples) (6)
Richardson.....	1921	Illinois.....	Littoral zone.....	.83 (weed beds) (7)
Richardson.....	1921	Illinois.....	Littoral zone.....	16.63 (weeds only) (7)
Meehan.....	1936	Louisiana.....	0-10 feet.....	1.03

(1) Good trout pond.

(2) Very good trout pond.

(3) Good salmon lakes.

(4) Canadarago Lake

(5) Otsego Lake.

(6) Bottom-land lakes.

(7) Glacial lakes.

All=Average of all depths.

tween total bottom fauna and fish production in his work on Alabama fish ponds. An unfertilized pond with a bottom fauna that averaged 19.62 milligrams of dry organic matter per square foot over a period of 22 weeks produced 147.1 pounds of fish per acre. An approximate conversion of Howell's work was made, based on data worked out by the writer and taken from other sources giving comparisons of volume of wet weight of organisms to dry organic matter. An approximate conversion of Howell's data for bottom fauna in terms of volume of organisms would give 0.30 gram per square foot for the unfertilized pond.

A fertilized pond having a bottom fauna with an average of 68.27 milligrams dry organic matter per square foot (approximately 1.03 grams per square foot wet weight) yielded 382.9 pounds of fish per acre.

Howell found, in comparing the food of bluegills from an unfertilized pond with that from a fertilized pond, that the fish from the fertilized pond had plenty of insects throughout the period considered (June through November) while those of the unfertilized pond had sufficient insects in June only. Examinations of stomachs of bluegills from these ponds showed that fish in ponds with an abun-

dant bottom fauna (fertilized) fed largely on insects throughout the period, whereas in the ponds having a limited supply of bottom fauna the principal food of the bluegills was *Najas*. Howell concluded that to increase fish production greatly the weight of bottom insects per square foot must increase rapidly as the growing season progresses. A survey of the literature shows that with few, if any, exceptions southern lakes and ponds are more productive of fish than comparable northern waters.

Third Sister Lake had an average of 1.17 grams of invertebrates per square foot as determined by dredge sampling for 1939 and 1940 and a fish population at the time of the poisoning of 86.6 pounds per acre. On the basis of direct comparison it would appear that Third Sister Lake is less productive of fish than either the Louisiana ponds studied by Meehean or the Alabama ponds studied by Howell. This can be explained to some extent by the longer growing season in the southern states and also by the fact that the entire area of the southern ponds was producing fish food. It was estimated that almost all of the invertebrate fish food (exclusive of plankton) was produced on 35 percent (3.5 acres of littoral zone) of the area of Third Sister Lake. When compared on the basis of actual productive areas, Third Sister Lake does not fall far short of the production of southern ponds. The data from Meehean, Howell, and the Third Sister Lake study are presented in Table 17. On the basis of 3.5 acres of productive area, Third Sister Lake produced 303.3 pounds of fish per acre. If this assumption is acceptable, it follows that a larger standing crop of invertebrates was necessary to maintain a given population of fish in Third Sister Lake and the southern ponds of Howell. This is perhaps explainable on the basis of more rapid replacement of the standing crop of invertebrates in southern waters. Miller (1941) estimates

TABLE 17—*Relationship of bottom fauna to fish production*

Investigator	Type of waters	Bottom fauna (pounds per acre)	Fish (pounds per acre)	Ratio of fish-food: fish
Meehean.....	Fertilized and unfertilized ponds (Louisiana).....	99.0	95.7	1:0.97
Howell.....	Fertilized ponds.....	98.0*	382.9	1:3.80
	Unfertilized ponds (Alabama).....	28.8*	147.1	1:5.10
Ball.....	Third Sister Lake, Michigan (3.5 acres)**	112.4	303.3	1:2.7

*An approximation. Original data in mg. dry organic matter.

**Area producing bulk of invertebrate fish-food organisms in Third Sister Lake.

that the standing crop of chironomid larvae is replaced eight or nine times during the summer in the epilimnion, depending on the number of day-degrees available for growth. Meehan's data is somewhat complicated by the fact that he does not record weight of forage fish taken from the ponds, which if added to weight of bass produced would raise the ratio of weight of fish to weight of fish food calculated from his data. Meehan (1936), experimenting with cottonseed meal as a fertilizer, found a relationship between the total weight of fish produced and the total weight of organisms when the weight of organisms is small enough to become a limiting factor. He obtained a production of 48 pounds of bass per acre when the weight of organisms was 5 grams per square meter. As the weight of organisms increased from 5 grams to 9 grams per square meter, the weight of bass per acre increased from 48 pounds to 105 pounds. When the weight of bottom organisms increased from 9 grams to 18 grams, the total weight of bass increased very little.

Richardson (1921) estimated the hypothetical yield of fish to be 289 pounds per acre for a bottom fauna of 1,447 pounds per acre in lakes of Illinois which gives a ratio of 1:5, or much less than actually was found in the studies by Howell, Meehan, and the present investigation on Third Sister Lake.

From the data available through this study, it is possible to estimate the quantitative relationship of the standing fish crop to the standing crop of fish-food organisms in this lake.

To make such a comparison, only those fish that have been shown by this and other food studies to be utilizing the bottom-dwelling organisms directly were considered. In Third Sister Lake, all fish except the largemouth bass and mud pickerel were considered to feed extensively on the bottom fauna.

From the food study it was determined that nearly all bottom fauna taken by the fish were produced in the area above the thermocline. This included the littoral (vegetated) zone and comprised approximately 3.5 acres (35 percent) of lake bottom.

The study of bottom fauna indicated an average standing crop of organisms of approximately 1.17 grams per square foot for the period of the year when the fish were feeding actively. This indicates an average standing crop of 393.3 pounds of invertebrate organisms for the lake.

From the population study it was determined that this food was

being utilized by a standing crop of 731 pounds of fish. By correlating the volume of invertebrate fauna in the lake with the rate of food consumption of these fish, the rate of removal of the available food can be determined.

If we assume that each fish consumes 1.2 percent of his own weight in food each 24 hours (Moore, 1941) and, as shown by the food study, approximately 50 percent of the food is from the bottom fauna, it then follows that the 731 pounds of fish will remove daily 4.38 pounds of bottom fauna, which is approximately 1.1 percent of the standing crop. This removal is more than equalled by the daily increase in the volume of the bottom organisms, which during September (1940) averaged 2.15 percent per day and in October of the same year averaged 3.55 percent.

The relationship between invertebrate production and fish population has been presented to show how data on invertebrate populations collected in routine lake surveys might be used in evaluating lakes as producers of fish. Work done on Third Sister Lake has not made possible the establishment of exact standards for evaluating other lakes with largemouth bass-bluegill populations but it is believed that this intensive study of the relationship of invertebrate fauna to the bass-bluegill population of one lake can stand as a basis of comparison for work on other lakes. From the comparison of bottom sampling data with studies of the growth rate of fish of the same lake and intensive sampling of lakes prior to the removal of unwanted fish populations, data may be established which will make possible estimating the pounds of fish being produced by a lake. It is suggested that any such correlation of data be based on the area of the littoral zone only and not on the total lake surface in lakes producing warm-water fish.

SUMMARY

1. While no single index of productivity for fish has been accepted by biologists, it appears that there is a definite relationship between the production of aquatic invertebrate fish food and the total production of fish.

2. A low volume of invertebrates per unit area of littoral zone indicates that the fish population has reached a point where it is consuming the available food at such a rate that these organisms cannot maintain themselves in a quantity great enough to support a growing fish population. The evidence from this study indicates that the

critical volume of aquatic invertebrates for this lake is approximately 1 cc. per square foot.

3. In using bottom- and plant-inhabiting invertebrates as a basis for comparing relative productivity of lakes, it is necessary to take into consideration the seasonal variation in number and volume of these organisms. A variation of 274 percent was found in the volume of organisms per unit area of lake bottom during the open-water season in Third Sister Lake.

4. It is suggested that lakes having a chemical stratification which results in a zone of oxygen depletion be compared on the basis of area of the littoral zone rather than total area of lake surface, inasmuch as the majority of the food utilized by warm-water fishes of such a lake is produced in that zone. The food study indicated that the littoral zone of this lake, constituting approximately 35 percent of the lake's surface area and 6 percent of its volume, produced the great majority of the food utilized by the fishes of the lake.

5. An average standing crop of invertebrates totaling 1.17 cc. per square foot of bottom area as determined by sampling in the littoral zone (3.5 acres), produced a fish population of 866 pounds of fish, of which 537 pounds were bluegills.

6. Bluegills, which feed on aquatic invertebrates during most of the active growing season, turn to plant food to supplement or replace animal food during the midsummer period when the volume of invertebrates reaches its lowest point of the year.

7. Selectivity of food organisms by bluegills was noted. Midge larvae were taken as food in a proportion greater than their relative abundance in the lake, whereas caddis larvae, a form which appears to be extremely available to the fish, were taken as food proportionately less than their relative abundance in the lake.

ACKNOWLEDGMENTS

The writer wishes to express his indebtedness to Prof. Paul S. Welch, Department of Zoology, University of Michigan, under whose direction this work was done; to the Institute for Fisheries Research, Michigan Department of Conservation, whose fellowship made the investigation possible; and to Drs. A. S. Hazzard and C. J. D. Brown, of the staff of the Institute for Fisheries Research, for advice and

criticism throughout the study. The writer is obligated to the School of Forestry and Conservation, University of Michigan, for permission to carry out the investigation of Third Sister Lake, and to Mr. Frank Murray, Forest Manager, for courtesies extended in connection with the work at the lake.

LITERATURE CITED

Allen, K. Radway

1941 Studies on the biology of the early stages of the salmon (*Salmo salar*). Jour. An. Ecol., 10: 47-76

1941 Comparison of bottom faunas as sources of available fish food. Trans. Am. Fish. Soc., 1941, 71: 275-283

American Public Health Association

1936 *Standard method for the examination of water and sewage*, Eighth Edition. Am. Public Health Assoc., New York, 309 pp.

Baker, Frank Collins

1916 The relation of mollusks to fish in Oneida Lake. Tech. Publ. 4, N. Y. State Coll. Forestry, 16: 1-366

Beckman, William C.

1940 Increased growth rate of rock bass, *Ambloplites rupestris* (Rafinesque), following reduction in the density of the population. Trans. Am. Fish. Soc., 1940, 70: 143-148

Growth rate of some Michigan game fishes. (Unpublished) Report, Institute for Fisheries Research, Ann Arbor

Bennett, Geo. W., Thompson, David H., and Parr, Sam A.

1940 A second year of fisheries investigations at Fork Lake, 1939. Ill. Nat. Hist. Surv. Biol. Notes, No. 14, 24 pp.

Brown, C. J. D. and Ball, R. C.

1940 A rowboat crane for hauling limnological sampling apparatus. Limnological Society of America, Spec. Publ., No. 3, 4 pp.

----- and -----

1942 (a) A fish population study of Third Sister Lake. Trans. Am. Fish. Soc., 1942, 72: 177-186

----- and -----

1942 (b) An experiment in the use of derris root (rotenone) on the fish and fish-food organisms of Third Sister Lake. Trans. Am. Fish. Soc., 1942, 72: 267-284

Burdick, G. E.

1940 Studies on the invertebrate fish food in certain lakes, bays, streams and ponds of the Lake Ontario watershed. Supp. 29th Ann. Rept., 1939, N. Y. Cons. Dept., pp. 147-166

Cooper, Gerald P.

- 1939 A biological survey of thirty-one lakes and ponds of the upper Saco River and Sebago Lake drainage systems in Maine. Fish. Surv. Rept. No. 2, Maine Dept. Inland Fish. and Game. 147 pp.

-
- 1940 A biological survey of the Rangeley Lakes, with special reference to the trout and salmon. Fish. Surv. Rept. No. 3, Maine Dept. Inland Fish. and Game. 182 pp.

-
- 1941 A biological survey of lakes and ponds of the Androscoggin and Kennebec River drainage systems in Maine. Fish. Surv. Rept. No. 4, Maine Dept. Inland Fish. and Game. 238 pp.

-
- 1942 A biological survey of lakes and ponds of Central Coastal Area of Maine. Fish. Surv. Rept. No. 5, Maine Dept. of Inland Fish. and Game. 184 pp.

Davis, H. S.

- 1938 Instructions for conducting stream and lake surveys. U. S. Bureau of Fisheries, Fisheries Circular No. 26, pp. 1-55

Deevey, Edward S., Jr., and Bishop, James S.

- 1941 Limnology. Sect. 2. A fisheries survey of important Connecticut lakes. Bull. 63, Conn. Geol. and Nat. Hist. Surv., pp. 69-121

Eggleson, Frank E.

- 1931 A limnological study of the profundal bottom fauna of certain freshwater lakes. Ecol. Monog. 1: 213-332

Hathaway, E. S.

- 1927 The relation of temperature to the quantity of food consumed by fishes. Ecol., 8: 428-434

Hess, A. D. and Swartz, Albert

- 1940 The forage ratio and its use in determining the food grade of streams. Trans. Fifth N. A. Wildlife Conf., pp. 162-164

Howell, H. H., Swingle, H. S., and Smith, B. V.

- 1941 Bass and bream food in Alabama waters. Alabama Cons., 1 (4): 3

Howell, Henry H.

- 1941 Bottom organisms in fertilized and unfertilized fish ponds in Alabama. Trans. Am. Fish. Soc., 1941, 71: 165-179

Klugh, A. B.

- 1926 The productivity of lakes. Quart. Rev. Biology, 1: 572-577

Leonard, J. W.

- 1941 Some observations on the winter feeding habits of brook trout fingerlings in relation to natural food organisms present. Trans. Am. Fish. Soc., 1941, 71: 219-227

Markus, Henry C.

- 1932 The extent to which temperature changes influence food consumption in largemouth bass (*Huro floridana*). Trans. Am. Fish. Soc., 1932, 62: 202-210

Meehean, O. Lloyd

- 1936 Some factors controlling largemouth bass production. U. S. Bur. Fish., Prog. Fish. Cult., 16: 1-6

McCormick, E. M.

- 1940 The study of some Reelfoot Lake fishes. Jour. Tenn. Acad. Sci., 10: 67-75

Miller, R. B.

- 1938 A statistical analysis of dredging data and notes on the bottom fauna of five Algonquin Park lakes. Unpublished Thesis, University of Toronto Library

Miller, Richard B.

- 1941 A contribution to the ecology of the Chironomidae of Costello Lake, Algonquin Park, Ontario, No. 49, Publ. Ont. Fish. Res. Lab. LX, 63 pp.

Moffett, J. W. and Hunt, Burton P.

- 1943 Winter feeding habits of bluegills and perch in Cedar Lake, Washtenaw County, Michigan. Trans. Am. Fish. Soc., 1943, 73: 231-242

Moore, Walter G.

- 1941 Studies on the feeding habits of fishes. Ecology, Vol. 22, No. 1, 1941

Mottley, C. McC., Rayner, H. J., and Rainwater, J. H.

- 1938 The determination of the food grade of streams. Trans. Am. Fish. Soc., 1938, 68: 336-343

Muttkowski, Richard Anthony

- 1918 The fauna of Lake Mendota. A qualitative and quantitative survey with special reference to the insects. Trans. Wis. Acad. Sci., Arts, and Lett. 19 (1): 374-482

Needham, P. R.

- 1928 A quantitative study of the fish food supply in selected areas. Suppl. 17th Ann. Rept., 1927, State of N. Y. Cons. Dept., pp. 192-208

Nevin, F. R.

- 1936 A study of the larger invertebrate forage organisms in selected areas of the Delaware and Susquehanna Watersheds. Suppl. to 25th Ann. Rept., 1935, State of N. Y. Cons. Dept., pp. 195-204

Pate, U. S. L.

- 1933 Studies on fish food in selected areas. Suppl. 22nd Ann. Rept., 1932, State of N. Y. Cons. Dept., pp. 130-156

-
- 1934 Studies on the fish food supply in selected areas of the Raquette Watershed. Suppl. 23rd Ann. Rept., 1933, State of N. Y. Cons. Dept., pp. 136-157
- Pearse, A. S.
- 1918 The food of the shore fishes of certain Wisconsin lakes. U. S. Bur. Fish. Bull., 35: 247-292
- Pentland, Ernest S.
- 1930 Controlling factors in the distribution of Gammarus. Trans. Am. Fish. Soc., 1930, 60: 89-94
- Richardson, R. E.
- 1921 The small bottom and shore fauna of the middle and lower Illinois River and its connecting lakes. Bull. Ill. Nat. Hist. Surv., 13: 362-522
- Scott, Will, Hile, Ralph O., and Spieth, Herman
- 1928 A quantitative study of the bottom fauna of Lake Wawasee (Turkey Lake). Publ. No. 77, Dept. of Cons., State of Indiana, 25 pp.
- Smith, E. V. and Swingle, H. S.
- 1940 Winter and summer growth of bluegills in fertilized ponds. Trans. Am. Fish. Soc., 1940, 70: 335-338
- Surber, E. W.
- 1930 A quantitative method of studying the food of small fishes. Trans. Am. Fish. Soc., 1930, 60: 158-163
-
- 1936 Rainbow trout and bottom fauna production in one mile of stream. Trans. Am. Fish. Soc., 1936, 66: 193-202
-
- 1938 A comparison of four eastern smallmouth bass streams. Trans. Am. Fish. Soc., 1938, 68: 322-335
-
- Swingle, H. S., and Smith, E. V.
- 1942 Management of farm fish ponds. Ag. Exp. Sta., Ala. Polytech. Inst., Bull. 254, 23 pp.
- Tarzwel, Clarence M.
- 1937 Factors influencing fish food and fish production in southwestern streams. Trans. Am. Fish. Soc., 1937, 67: 246-255
- Townes, H. K., Jr.
- 1938 Studies on the food organisms of fish. Suppl. 27th Ann. Rept., 1937, State of N. Y. Cons. Dept., pp. 162-173



SERVING MICHIGAN

WKAR (870) - WKAR - FM (90.5)